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***Elpiscladius* Harrison and Cranston, a new orthoclad (Diptera: Chironomidae) in the Brillia-group from South Africa**

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An extensive survey of South African larval and pupal Chironomidae has revealed a previously unknown taxon in the subfamily Orthoclaadiinae. The material comprises three pupal exuviae and one pupa containing a pharate adult male, the morphology of which is readily observable. *Elpiscladius capicola* Harrison & Cranston, **gen. et sp. nov.** is described and illustrated based on the pharate adult and pupal exuviae. The male hypopygium has a divided gonostylus, the eye has a dorsomedial extension, and the body is highly setose; evidently the new genus belongs to the Brillia-group of genera. Pupal morphology does not refute such a relationship, and phylogenetic analysis of the combined adult and pupal morphology indicates the new genus to be the sister group of *Austrobrillia* Freeman (*Euryhapsis* Oliver+*Eurycnemus* van der Wulp). Based on the phylogenetic position of *Elpiscladius* gen. nov., the as yet unknown larva is predicted to be either leaf- or wood-mining.

Keywords: Orthoclaadiinae, new genus, new species, systematics, biogeography.

INTRODUCTION

The distributions of Southern Hemisphere Chironomidae (Diptera) have been influential in studies of historical biogeography and ecology, including reconstructions of past environments (e.g. Brundin 1966; Cranston 1994b).

The significance of South African chironomid distributions and their relationships to the biota of other southern continents was recognised by Freeman (1961: 613–614) and Brundin (1966: 452). Stemming from distributions on the southern land masses that comprised Gondwana in the Jurassic/Cretaceous, many modern distributions apparently retain the signal of their deep history. As illuminated, particularly by Brundin (1966), Gondwanan distributions are revealed in the subfamilies Podonominae and Aphroteniinae, and in the tribe Heptagyiini of the subfamily Diamesinae. Similar patterns are being revealed in the subfamilies Tanypodinae, Orthoclaadiinae and Chironominae. However, these patterns either preclude southern Africa, or if the region is included, their extralimital relationships often connect *via* the afro-montane and Rift Mountains to the Palaearctic, rather than to other austral areas.

The writers have discovered independently a pharate male within a pupa (by A.D.H.), and pupal exuviae (cast skins) intercepted in drift (by P.S.C.), of a species evidently

belonging to the Brillia-group; a clade of Orthoclaadiinae rare in the Afrotropical Region. This taxon warrants description, even in the absence of larvae, adult females or emerged males. Thus, we describe here a pharate adult male retained within its pupal exuviae, and exuviae, all derived from the Western Cape Province of South Africa. An existing taxon-character matrix compiled to examine the relationships in the Brillia-group (Cranston 2000) is expanded upon to include this new South African genus, and parsimony analysis is applied to determine phylogenetic relationships.

MATERIAL AND METHODS

Ideally, associated larvae, pupae and female adult stages are preferred for full taxonomic descriptions; these have, however, proven highly elusive for this chironomid species. No candidate larvae recognisable as belonging to the Brillia-group have been identified amongst thousands of specimens examined by the first author. Fortuitous association of larval head capsule still attached to a pupa is rendered unlikely, given the paucity of pupal exuvial specimens encountered by the second author while drift-netting numerous 'suitable' streams in the Western Cape Province. It is decided, therefore, to present the description of this new taxon based on available stages only.

Standard morphological terminology and abbreviations follow Sæther (1980) and Cranston (1994a), with 'taenia' (adjective 'taeniate') used for the broadened pupal setae (Langton 1994). The term 'distolateral lobe' is preferred for the more distal gonocoxite lobe following Oliver's (1985) scepticism concerning homology with the inferior volsella. In the pupa, the conjunctive is numbered as belonging to the segment anterior to it. Unless otherwise indicated, measurements are in μm , generally rounded to the nearest $5\mu\text{m}$, except in cases where measurement at maximum magnification provided greater accuracy.

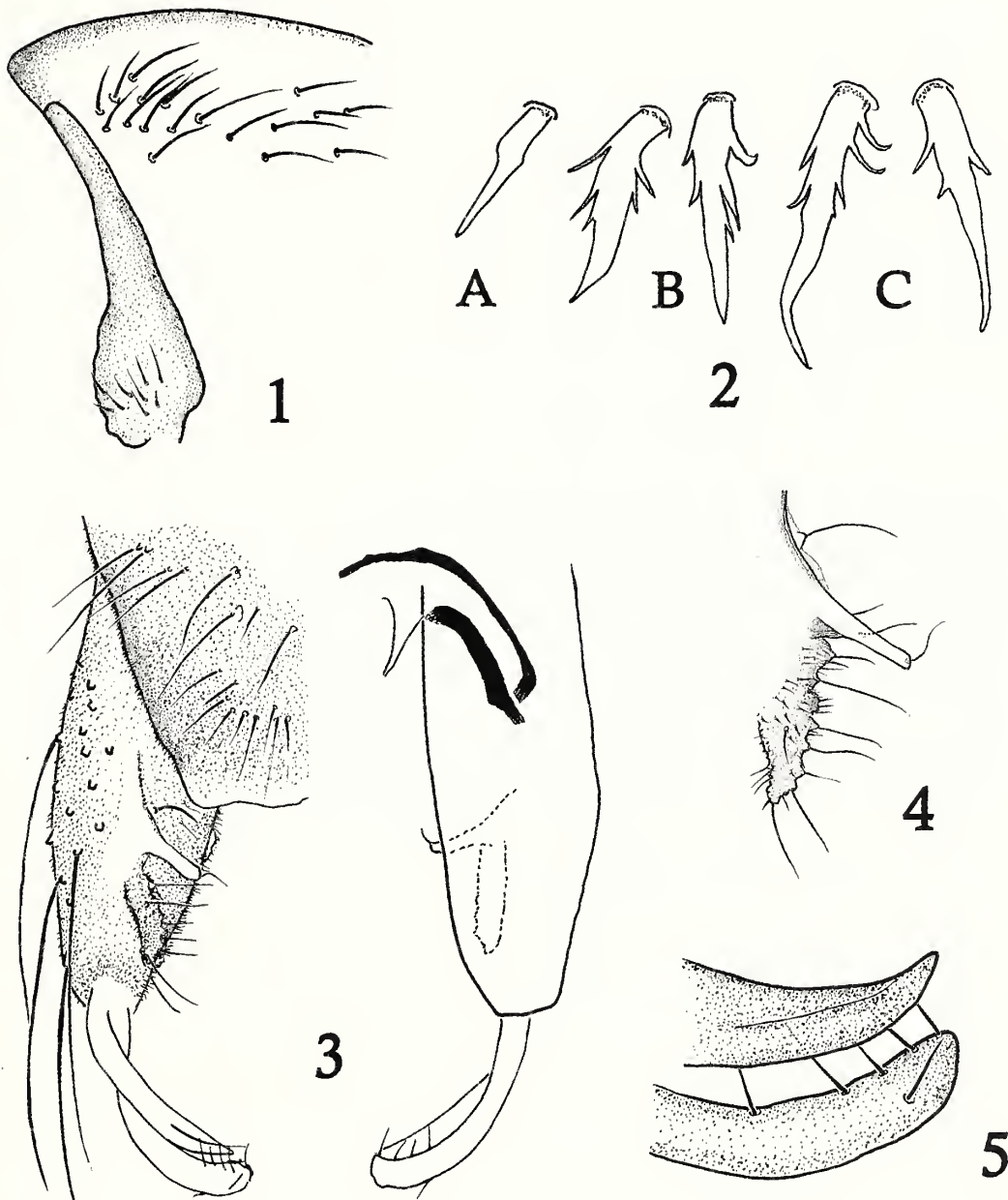
The holotype (pharate male) was mounted from 96% ethanol into Canada balsam dissolved in cellosolve, uncleared (by A.D.H.); exuviae were mounted from isopropanol in euparal (by P.S.C.). Material is housed in the Albany Museum, Grahamstown, South Africa (AMGS), the Natural History Museum, London, United Kingdom (BMNH), and the Australian National Insect Collection, CSIRO, Canberra City, Australia (ANIC).

SYSTEMATICS

ELPISCLADIUS HARRISON & CRANSTON, GEN. NOV.

Type-species: *Elpiscladius capicola* Harrison & Cranston, sp. nov., by monotypy.

DIAGNOSIS: The adult male of *Elpiscladius* gen. nov. is diagnosed by the attenuated



Figures 1–5. *Elpiscladius capicola* gen. et sp. nov. Adult male: 1, anterior thorax, lateral; 2, tibial spurs – A. fore, B. mid, C. hind; 3, hypopygium, left side dorsal, right side internal/ventral; (stylised) 4, superior volsella and distolateral lobe; 5, apices of gonostylus.

anteprenotal lobes, without dorsal anteprenotals, lack of pulvilli and tibial comb, in combination with a hypopygium without anal point, with bifid gonostylus lacking megasetae, and with a digitiform superior volsella. The pupa has frontal setae, spinose thoracic horn, hook row on tergite II, no taeniate L setae, spinose apical anal lobe, 3 macrosetae amongst a dense anal lobe fringe, and characteristic long seta on the anal lobe inner margin.

DESCRIPTION OF ADULT MALE: Antenna with 13 flagellomeres. Eye bare, with parallel-sided dorsomedian extension 7–8 facets deep. Palp 5-segmented, with segment 1 distinct, 4 and 5 subequal. Anteprenotal lobes widely-separated medially, narrow ventrally, with lateral anteprenotal setae only; scutum slightly overreaching anteprenotum. Acrostichals absent; dorsocentrals multiserial, long and numerous, beginning at anterior margin; few prealars; very long uni-biserial scutellars. Wing rather narrow, with minimal anal lobe, densely clothed in numerous fine macrotrichia, R-M apparently long and oblique, R_{4+5} ending before wing margin; costa non-extended; squama with uniserial fringe. Legs with single spur on foretibia, with well developed tibial spurs on mid and hindlegs, spurs of each pair subequal in length, lateral spines diverging from shaft of spur, lacking hindtibial comb; claws simple and pointed, pulvilli absent. Hypopygium without anal point; transverse sternapodeme narrow, inverted U-shaped without projection or ridge; phallapodeme stout, with indication of median attachment to weakly sclerotised phallus, but lacking virga. Gonocoxite with two connected lobes, more anterior (superior) digitiform, medially-directed, non-microtrichiose, linked basally to caudally-directed setose and microtrichiose distolateral lobe. Gonostylus narrow and bifurcate, lobes of subequal length, setae few, only on apical lobe, lacking megaseta.

DESCRIPTION OF PUPA. Medium-sized, 4.4–7.2 mm long, pale yellow with slightly darker lateral and transverse apophyses.

Cephalothorax: frontal setae on weakly crenulate frontal apotome. Ocular field with 1 postorbital, without vertical seta. Thorax with 2 median anteprenotals (aps), 1 lateral aps, 3 subequal precorneals; 4 stout, equidistant dorsocentrals, Dc_4 longer than more spine-like Dc_{1-3} . Thoracic horn broadening to middle, apically pointed, with variable density and size of spinules covering at least apical half. Dorsal thorax smooth. Prealar area rectangular, bare. Wing sheath without pearl row.

Abdomen: Tergite I bare, TII–VI evenly spinulose, TVII and VIII with minor anterior spinulation. TII with uni-, weakly biserial hook row; conjunctives III and IV spinose in transverse multiserial band narrower than preceding tergal armature. Sternites anteriorly with fine transverse spinulation, plus stronger pleural stripes on IV. Pedes spurii A moderately developed on IV, weaker on V and VI. Anal lobe elongate oval, with

sparse anterior shagreen; fringe taeniae uniserial anteriorly, multiserial posteriorly, with 3 macrosetae inserted subapically, 1 long median seta. Apex of anal lobe beset with stout spines. Male genital sac very elongate tapering to rounded point, extending far beyond anal lobe apex, containing very elongate gonocoxal setae.

Abdominal setation: Segment I with 5D, 4V; 2L; segments II–VII with 5D, 4V; 4L, of which L4 is significantly postero-lateral; segment VIII with 1D, 1V and 5L, all longer and stouter than on more anterior segments, but none taeniate. Dorsal O-seta lie between transverse apodeme and conjunctive, ventral O-seta on transverse apodeme.

ETYMOLOGY: The generic epithet *Elpiscladius*, is derived from the Greek ‘*elpis*’ meaning ‘hope’, referring to the Cape of Good Hope.

***Elpiscladius capicola* Harrison & Cranston, sp. nov.**

MATERIAL EXAMINED: Holotype pharate male, SOUTH AFRICA, Western Cape, Betty’s Bay, Harold Porter Botanical Gardens, Davidskraal River, 34°20'50"S, 18°55'17"E, 29.i.1997, Denise Schael (AMGS, ABLDK.9C). Paratypes, 1 pupal exuviae, SOUTH AFRICA, Western Cape, Jonkershoek Nature Reserve, upper Eerste R., 33°59'38"S, 18°58'30"E, 22.xii.1996, P.S. Cranston (BMNH); 1 pupal exuviae, same except: 29.i.1998 (BMNH); 1 pupal exuviae, same except: 15.x.2005 (ANIC).

DESCRIPTION: [based on one well-developed pharate male and three pupal exuviae].

ADULT MALE ($n=1$, pharate within exuviae).

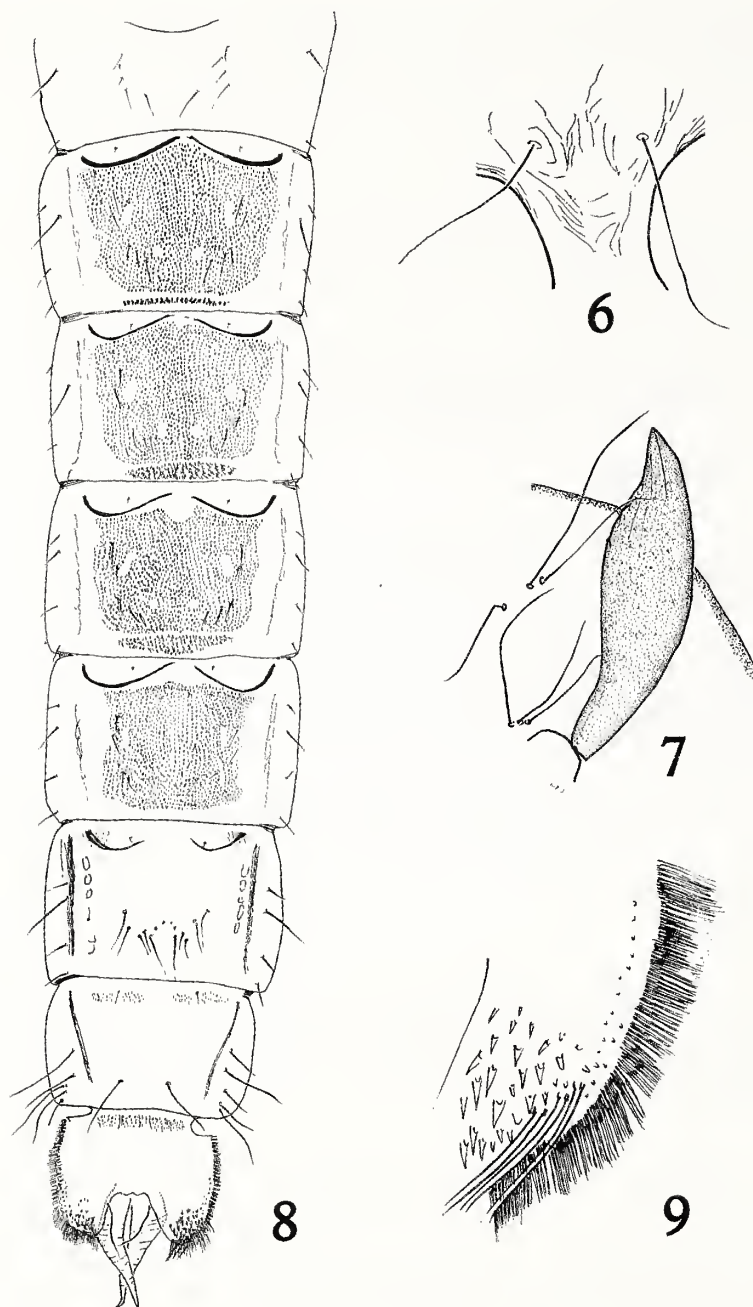
Body length: 4.2 mm.

Head: Antenna with 13 flagellomeres; basal flagellomeres c 35 long, apex of terminal flagellomere hidden by leg sheaths: AR incalculable. Eye bare with parallel-sided dorsal extension; temporal setae 16–18, more or less uniserial; palp with segment 1 distinct, lengths 20, 40, 76, 80, 95.

Thorax: Anteprenotal lobes widely separated (Figure 1), 8–9 lateral anteprenotals, no dorsal setae; anterior margin of scutum slightly overreaching anteprenotum. Acrostichals absent, c 50–56 long multiserial dorsocentrals, 8 prealars, supraalars not visible; 18 very long scutellars extending almost to posterior tip of postnotum (within exuviae).

Wing: Membrane densely clothed in short, fine setae. R_{4+5} apparently ending prior to wing margin, without costal extension. Squama with 16 setae.

Legs: Densely setose. Tarsomere 1 on each leg with longest setae 3–4 times tarsomere diameter. Spurs (Figure 2): foretibial 37 long, midtibiae 55, 60 long, hindtibiae 62, 74



Figures 6–9. *Elpiscladius capicola* gen. et sp. nov. Pupa: 6, cephalic area; 7, thoracic horn, anteprenotals and precorneals; 8, abdominal tergites (anal lobe fringe attenuated); 9, anal lobe, detail.

long; mid and hind spurs with 2–3 lateral spines divergent from shaft, hind tibia lacking comb. Pseudospurs and sensilla chaetica absent, tarsomere 4 cylindrical and longer than tarsomere 5, claws simple and pointed, pulvilli absent.

Hypopygium (Figures 3–5). Tergite IX squat with numerous long setae, no anal point, virga absent. Apodemes as in Figure 3. Gonocoxite 205 long, almost parallel-sided, inner margin (Figure 4) bearing two lobes: superior volsella small and narrow with 1 ventro-medial, and 1 terminal seta; distolateral lobe microtrichiose and setose, arising appressed to base of superior volsella and inner gonostylus, distally free for at least half length. Gonostylus bilobed (Figures 3, 5); lobes narrow, of subequal length 104 long, ventral lobe bare, arising near base of dorsal lobe, apical lobe with several terminal setae. See generic description above for further details.

PUPA ($n=4.3$ exuviae)

Hyaline to very pale yellow with darker yellow, medially interrupted, dorsal and ventral transverse apophyses; lateral apophyses darker yellow-brown.

Length 4.4–7.2 mm.

All cephalic and thoracic setae strong, but non-taeniate: frontal setae (Figure 6) 150–250 long; anteprenotal setae: $Maps_1$ 175–260 long, $Maps_2$ 175–260 long, $Laps$ 115–165 long; precorneals approximated and linearly aligned, subequal, 190–210 long; dorsocentrals: Dc_1 25–50 long, Dc_2 12–25 long, Dc_3 33–50 long, De_4 55–75 long; distances Dc_{1-2} 115–125, Dc_{2-3} 120–150, Dc_{3-4} 20–35. Thoracic horn (Figure 7) 310–470 long, broadened medially, somewhat tapered apically, weakly to densely spinose.

Abdominal tergites as in Figure 8; anal lobe as in Figure 9, with inner marginal seta 110–135 long, 74–99 taeniae, up to 600 long, with macrosetae differentiated by being somewhat broader and darker, and much shorter (250 long).

ETYMOLOGY: The specific epithet *capicola* refers to its dwelling in the Cape.

VARIATION: There is substantial size difference between the type specimen, of length 4 mm, and the three exuviae with lengths of 6–7 mm. This is reflected somewhat in the lengths of the thoracic horn which is 50% longer in the exuviae and more densely spinose. The largest pupa also has the anal lobe with larger and more numerous subapical spines, and generally darker apophyses. Setal lengths also vary in like manner. These mensural differences are considered, *prima facie*, to represent allometric differences, perhaps associated with different developmental conditions, such as temperature (McKie & Cranston 2005).

PHYLOGENETIC RELATIONSHIPS

Elpiscladius gen. nov. evidently belongs in a group of genera centered on *Brillia* Kieffer (the Brillia-group of Sæther & Wang 1992; Cranston 2000), based on the adult male having a strongly setose body, setose wing membrane with R-M long and oblique, dorsomedially extended eye, and hypopygium with characteristic digitiform superior volsella and bifurcate gonostylus. The pupa of this group is poorly defined, but the stout, spinose thoracic horn, strongly developed apophyses and subapical macrosetae on a strongly fringed anal lobe conform with many contained taxa. The male resembles that of the Holarctic *Eurycnemus* van der Wulp (Cranston *et al.* 1989; Kobayashi 1998), particularly regarding the separated anteprenotal lobes, lack of tibial comb and lack of anal point. Differences, however, include the short wing membrane setae, the shorter extension of the scutum beyond the anteprenotum, the lack of dorsal anteprenotals, the mid- and posterior tibial spurs being subequal and the lack of pulvilli. In some features, *Elpiscladius* gen. nov. more closely resembles the Australian-Neotropical *Austrobrillia* Freeman and Holarctic *Euryhapsis* Oliver. The pupa of *Elpiscladius* gen. nov. fails to key in Coffman *et al.* (1986) and in Sæther *et al.*'s (2000) key expanded therefrom: problems derive from irreconcilable character conflicts including non-taeniate lateral setae on posterior segments, simple (non-divided) thoracic horn, and presence of only 3 macrosetae on the anal lobe. Nonetheless, *Elpiscladius* gen. nov. has the 'gestalt' of pupa belonging to the Brillia-group. The inner marginal seta of the pupal anal lobe is unusual, having been observed previously only in *Tvetenia* Kieffer, and the Corynoneura-group (*Corynoneura* Winnertz, *Tempisquitoneura* Epler, *Thienemanniella* Kieffer, *Notocladius* Harrison and *Oucouneura* Anderson & Sæther) (Anderson & Sæther 2005). There is no evidence that this feature links *Elpiscladius* gen. nov. to this grouping, and the presence of the seta must be considered homoplasious.

To address the issue of relationships better, a character matrix used by Cranston (2000) to assess the relationships of *Austrobrillia* Freeman, has been extended to include *Elpiscladius* gen. nov. One character was added: the anteprenotal lobe shape, with an attenuated and well-separated state, previously considered to be autapomorphic for *Eurycnemus*, was scored as present also for *Elpiscladius* gen. nov. This matrix (available from Cranston on application) contains all taxa which bear any likely relationships to the Brillia-group, irrespective of which life history stages are known. In addition, taxa postulated to be among the earlier branching lineages in Orthoclaadiinae are represented. *Prodianesa* Kieffer (Prodianesinae) was used as outgroup, and the data analysed under parsimony with PAUP* (Swofford 2002). The matrix contains many unknown states for missing semaphoronts, as for example *Elpiscladius* gen. nov. which is unknown as larva or adult female. However, previous studies (Cranston 2000) indicate that inclusion/exclusion of incompletely known taxa does not alter major relationships based

upon the fully known taxa alone. As seems usual with morphological matrices, resultant trees are of low consistency, retention and bootstrap; however, all recover *Elpiscladius* gen. nov. as sister to the clade *Austrobrillia* (*Euryhapsis*+*Eurycnemus*). In turn, this clade is sister to a poorly resolved group containing the remaining Brillia-group (*sensu* Sæther & Wang 1992), including *Brillia*, *Irisobrillia* Oliver, *Neobrillia* Kawai, *Plhudsonia* Sæther, *Tokyobrillia* Kobayashi & Sasa and *Xylotopus* Oliver.

Although the larva of *Elpiscladius* gen. nov. is unknown, its postulated phylogenetic placement allows some speculation as to its likely morphology. The known larvae of this group, which are more homogeneous than the pupae, all have a 4-segmented antenna with squat apical segments, a heavily sclerotised mentum and a mandible with reduced number of teeth.

BIOGEOGRAPHY AND ECOLOGY

In reviewing the biogeography of Afrotropical Chironomidae, Sæther & Ekrem (2003) suggested that a species of *Tokyobrillia* from Usambara, in the Eastern Arc Mountains of Tanzania, which is clearly a close relative to a Japanese congener, evidently was the sole African representative of genera near *Brillia* or *Irisobrillia*. The discovery of *Elpiscladius* gen. nov., however, indicates that there is a wider representation. Although reconstruction of the phylogeny of the Orthoclaadiinae remains tentative, with much homoplasy and uncertainty concerning the details, there is an emerging agreement that the Brillia-group is monophyletic and represents an early branch ('basal', 'primitive'), perhaps forming the sister group to the remaining Orthoclaadiinae (Cranston 2000; Sæther & Wang 1992). Such a placement is substantiated by a multigene molecular phylogeny (Morse & Cranston in prep), although this study utilises a smaller taxon sample. The emerging phylogeny implies an early origination of a differentiated Brillia-group, which combined with the almost global distribution, implies a Pangaeon distribution, with subsequent diversification associated with tectonism, including Gondwanan fragmentation. The close association with *Austrobrillia*, known from Australia and the Neotropics, plus two widely distributed Holarctic taxa, provides additional support for early radiation.

An alternative interpretation for the presence of Brillia-group members in southern Africa is that they belong to groups of chironomids that made their way down the mountain spine of Africa after the continent joined Eurasia, with rifting since the Miocene creating semi-continuous suitable habitat for chironomids (Harrison 1992; Harrison & Hynes 1988). Such a scenario was proposed, derived from the phylogeny of essentially northern *Diamesa*, by Willassen & Cranston (1986). As with *Diamesa*, generally taxa that extend from the palaearctic to southern Africa appear to be more recent intruders into Africa in cosmopolitan groups (Sæther & Ekrem 2003), and seemingly with shallow phylogenetic differentiation from their northern relatives.

Elpiscladius gen. nov. has been found in only two mountain streams in the Cape Fold Mountains of the Western Cape. The taxon appears to be rare in that only single exuviae have been found amongst drift net samples accumulated overnight on three separate occasions – thereby comprising less than 1% of the chironomid exuviae collected on each occasion. The clade to which *Elpiscladius* gen. nov. belongs includes both leaf- and wood-miners, and larval associates with cased caddis flies (e.g. Cranston 2000; Kobayashi 1998), and it might be expected that the unknown larva occurs in one of these under-sampled habitats.

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A reappraisal of the type fossil of *Curtonotum* †*gigas* Théobald, 1937 (Diptera: Curtonotidae), a compression fossil of Early Oligocene age from Provence, France

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The fossil type of *Curtonotum* †*gigas* Théobald, 1937, from Early Oligocene deposits in Les Camoins, Provence, France, is re-evaluated and its status and placement is discussed, compared to diagnoses of the family Curtonotidae and the genus *Curtonotum* Macquart. Digitised images of the fossil are provided and these are compared in detail to digitised images of diagnostic character states of the genus *Curtonotum*, as currently recognised. Key character states required for the determination of the family are not discernable on the fossil type, due to the very poor state of preservation, and it is not possible to ascribe the species to either the Drosophilidae *sensu stricto* or Curtonotidae (as previously suggested). As the species cannot be ascribed to a family, it is treated as *insertae sedis*.

Keywords: Curtonotidae, *Curtonotum*, taxonomy, Early Oligocene, diagnoses, fossil record.

INTRODUCTION

Grimaldi & Engel (2005: 547) date the origin of the Schizophora, to which the family Curtonotidae belongs, in the latest Cretaceous to earliest Tertiary, about 65 MYA, but with their radiation exclusively in the Tertiary.

The acalyptrate family Curtonotidae represented by three extant genera worldwide, is extremely poorly represented in the fossil record (*vide* Evenhuis 2006). Only a single fossil is known; namely that of *Curtonotum* †*gigas* Théobald, 1937, a compression fossil of Early Oligocene age from Les Camoins (*ca.* 43°17'S, 5°30'E), near Marseille, Provence, France (Figure 1).

This specimen originates from outcrops of lacustrine sediments that are made up of fine laminated limestones and inter-bedded gypsum. The age of these rocks is given as Early Oligocene (*ca.* 33.9 MYA), as indicated in a recent revision of the Oligocene of Provence (J. Philip pers. comm.). These deposits are rich in fossils, especially those of insects and plants, and the descriptions of insects of several orders have previously appeared in the literature (e.g. Théobald 1937; Timon-David 1944).

Théobald (1937) provided a brief description of *C.* †*gigas* (pp. 288–289), and a line drawing of the specimen (Plate XX, fig. 8; Figure 3, this paper). As both the description and figure do not refer to, or appear to illustrate, diagnostic character states of either the family Curtonotidae or the genus *Curtonotum* Macquart, 1844, it was desirable to re-examine the specimen and assess its validity in terms of familial and generic placement.

MATERIAL AND METHODS

Images of the fossil were captured using a Canon® EOS 10D digital camera with a 50 mm macro lens and of the extant *Curtonotum tigrinum* Séguy, 1933, with a Leica® EZ4D binocular microscope with in-built digital camera. These were saved digitally and were cleaned and enhanced using the computer program Coral Draw®.

It should be noted that comparison of the fossil type of *C. †gigas* with extant species of Curtonotidae was based on the examination of digitised images captured using light microscopy only. Examination using polarising filters was not undertaken, as the poor state of preservation of the specimen did not allow such examination.

Holotype label data are quoted as they appear; a division slash (/) indicates the end of a line of print, double division slash (//) signify data on a further label. Significant supplementary or qualifying information is presented in square brackets when considered necessary. Abbreviations used in the text: 'Figure' or 'Figures' as cited in the text refers to figures cited in this paper; 'fig.' to 'figures' in other publications. NMWC = National Museum & Gallery of Wales, Cardiff, United Kingdom.

Terminology of the external morphology follows, for the most part, that of the interactive *Anatomical Atlas of Flies* (Yeates *et al.* 2004). For head bristles not defined in that work, terminology follows Barraclough (1995: 100), and abbreviations for dorso-central bristles follow Tsacas (1977: 148).

RESULTS AND DISCUSSION

PAST INTERPRETATIONS

Théobald's (1937) original French description of *C. †gigas* reads: <Insecte de petite taille, assez mal conservé, teinte brun foncé. Tête écrasée: yeux encore visibles; thorax noirâtre, fortement renflé sur le dos. Abdomen nettement séparé, forme ovale, 7 segments; pattes grêles, hanches longues, fémurs forts, velus; tibias allongés, cylindriques, munis de soies, tarses grêles. Ailes dépassant l'abdomen, nervures Sc et R accolées, se terminant avant le milieu de l'aile: on voit ensuite 4 nervures longitudinales, les 2^e et 3^e embrassant le sommet de l'aile, les nervures divergeant à peu près régulièrement, les nervures transversales ne sont pas visibles. Dim.: L du corps = 5 mm.> The English translation reads: Insect of small size, poorly conserved, dark brown colouration. Head crushed, eyes still visible; thorax blackish, strongly swollen on the back. Abdomen clearly separated, oval shaped, 7 segments; legs long and thin, hips long, femora strong, hairy; tibia elongated, cylindrical, covered with setae; tarsal segment long and thin. Wings reaching beyond abdomen, veins Sc and R fused, ending before middle of the

wing: one observes furthermore 4 longitudinal veins, the 2nd and 3rd embracing the tip of the wing, the veins diverge rather regularly, cross-veins not visible.

Dimensions: length of the body – 5 mm. (translation by Marc De Meyer).

Théobald's (1937) illustration of the fossil (reproduced here as Figure 3), exhibits a good deal of artistic licence, in terms of the accuracy of illustrated structures; especially the wing and legs.

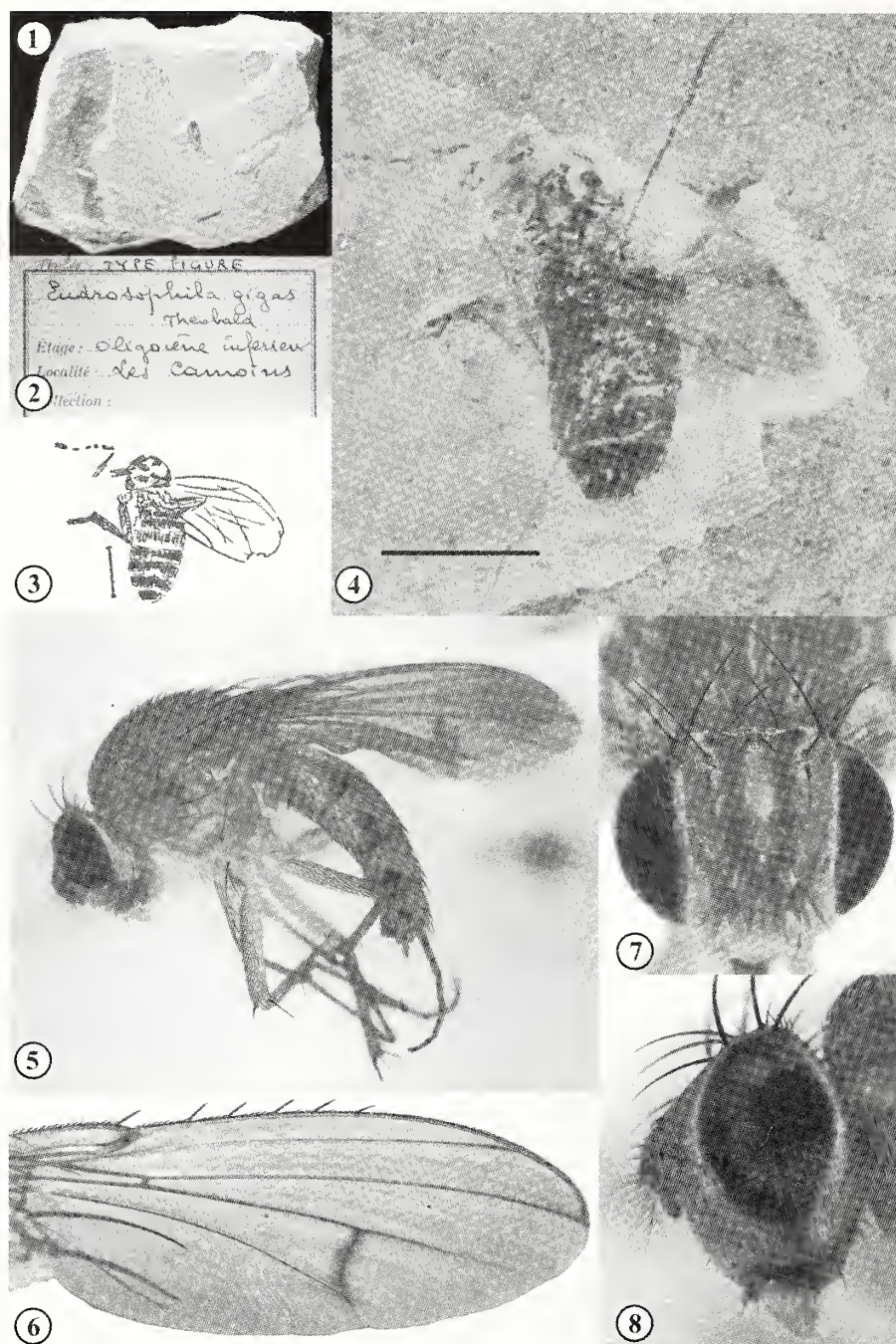
In his description Théobald (1937: 289), tentatively assigned *C. †gigas* to the genus *Curtonotum* (as “(?) g. *Cyrtonotum* MACQUART”), but further remarked that the specimen was originally identified as the [Oriental] genus *Eudrosophila* Malloch, 1924 (Drosophilidae), by Eleazar Abeille de Perrin (1843–1910), although this remained unpublished < ... cet échantillon a été déterminé *Eudrosophila gigas* par le Dr Ab. de Perrin, mais est resté inédit. Il appartient aux *Drosophilidae*; il se distingue facilement des *Drosophiles* par la taille assez considérable.> It should be noted that at the time the description appeared the Curtonotidae were regarded as a subfamily of the Drosophilidae: the Cyrtonotinae.

Théobald notes his reasons for tentatively ascribing *†gigas* to the Curtonotidae (as Cyrtonotinae), rather than to the Drosophilidae *sensu stricto*, as being the considerable size of the fossil (Curtonotidae being ‘4–5 mm’), the strongly swollen mesonotum, the simple venation, and the more elongated shape of the abdomen <Les *Cyrtonotinae* par contre ont une taille voisine, 4–5 millimètres; *Cyrtonotum anus* MEIGEN a aussi le mésonotum fortement renflé, la nervation de l’aile est semblable, mais l’abdomen a une forme plus allongée.> This highly superficial characterisation of both the family and the genus is clearly insufficient to ascribe the fossil specimen to either taxon by modern taxonomic standards.

In order to compare the fossil specimen of *C. †gigas* to extant representatives of the family Curtonotidae, and specifically the genus *Curtonotum*, it is first necessary to diagnose the two taxa and to list external morphological characters which in combination define them.

FAMILY: CURTONOTIDAE DUDA, 1924:

Diagnosis. The family Curtonotidae can be diagnosed as follows (based on Marshall *et al.* (in press), with amendments): Small to medium-sized (4–9 mm), distinctively robust flies, with a hump-backed, drosophilid- or heleomyzid-like form, usually greyish to yellow, often with spots, strips or irrorations on the thorax and pigment patterns on the abdomen. Arista plumose, with long dorsal and ventral rays; rays varying in number. Wing pigmentation varying from hyaline to lightly fumose (especially on r-m and dm-cu crossveins), or boldly patterned; subcosta complete, cell cup present, cells dm and bm confluent, and costa (c) with humeral and subcostal breaks. Abdomen with aedeagus enlarged, C-shaped, distiphallus anteroventrally-directed; two spermathecae present.



Figures 1–4. Early Oligocene fossil of *Curtonotum* †*gigas* Théobald from Les Camoins, Provence, France. 1, habitus of fossil in laminated limestones and inter-bedded gypsum; 2, Holotype label; 3, line drawing of *Curtonotum* †*gigas* from Théobald (1937: Plate XX, fig. 8), scale bar length unspecified, but probably 0.5 mm.; 4, detail of fossil, scale 0.5 mm. Figures 5–8. *Curtonotum tigrinum* Séguy, an extant species. 5, habitus, lateral aspect; 6, right wing, from above; 7, head, anterodorsal aspect; 8, head in profile. Not to scale.

GENUS: *CURTONOTUM* MACQUART, 1844

Type species: *Musca gibba* Fabricius, 1805 [preoccupied = *Curtonotum taeniatum* Hendel, 1913], by original designation.

Figures 5–8.

Diagnosis The genus *Curtonotum* can be diagnosed as follows (based on Tsacas (1977), with amendments): *Head* (Figures 7, 8): with two pairs of long, prominent fronto-orbital bristles, the anterior pair (or1) (those closest to antennal bases) proclinate, the posterior pair (or3) reclinate, with a minute reclinate seta (or2) positioned between them close to base of or3; frons wide in both sexes. *Thorax* (Figure 5): Scutum more-or-less hump-backed in appearance, with a pair of strong dorso-central bristles and one pair of acrostichal bristles; anepisternum with 2–3 long bristles and some short setae; one very long katepisternal bristle accompanied by a short anterior one. *Scutellum* entirely covered in hairs, with two pairs of strong marginal bristles. *Wing* (Figure 6): greyish to grey-brown infusate, dm-cu crossvein usually markedly infusate; costa (c) with humeral and subcostal breaks, and with a variable number of prominent costal spines beyond R₁ longer and stronger than adjacent vestiture. *Legs*: all tibiae with preapical dorsal bristles; forefemur with row of short, but strong spinules along distal half or third, variable in number. *Abdomen* (Figure 5): long, cylindrical, generally pale in colour with brown spots or T-shaped inverted lateral markings. Basiphallus and distiphallus fused and asymmetrical. Spermathecae flattened, short and obclavate with a folded or rugose surface or long, tubular and studded with protuberances.

MATERIAL EXAMINED

Type material examined:

Curtonotum †*gigas* Théobald, 1937. Holotype (unsexed): “Th24 TYPE FIGURE / *Eudrosophila gigas* / Theobald / Étage: Oligocène inferieur / Localité: Les Camoins / Collection: [hand-written & printed with black border; *vide* Figure 2] // 926 Th 24 Type figure / *Eudrosophila gigas* / CYRTONOTUM Theobald / Étage: Oligocène inf. / Localité: Les Camoins / Collection: [hand-written & printed]” // same except: “1613 926” [red disc in top right hand corner] (Museum de Paléontologie de Provence, Université de Provence, France).

Comparative material examined:

Curtonotum tigrinum Séguy, 1933. 1♂, 1♀, N. Nigeria, River Bagel at crossing of Bauchi-Dass road, 3.iv.1990, J.C. Deeming, roosting in moist cave in bank of dry river, NMW.Z.1981–001 (NMWC).

RE-INTERPRETATION AND COMPARISON

Given the incomplete structure of the fossil and the very poor state of preservation, it is only possible to study a limited number of structures of the external morphology, regarded as diagnostic for the family and genus; these being the wing, abdomen, foreleg and hindleg.

The head is either flattened beyond recognition or is entirely missing, and what was regarded by Théobald as the crushed head may, in fact, be derived from thoracic fragmentation. The absence of the head precludes examination of key character states diagnostic for the family Curtonotidae and the genus *Curtonotum*, such as frons width, number and arrangement of fronto-orbital bristles (Figure 7), and the arista (to assess the presence and degree of plumosity of the upper and lower surfaces) (Figure 8). The absence of the head is the single most important limiting factor to the correct determination of the specimen.

Due to excessive compression, the thorax is too flattened and expanded to make a true assessment of the degree of convexity as it would have appeared in an unaltered state (e.g. as in Figure 5). Such a character is, in isolation, of little or no taxonomic value, as a hump-backed appearance is apparent in numerous species of Diptera in various families, including the closely-related drosophiloid families Diastatidae, Campichoetidae and some Drosophilidae. Identification is further hampered by the dorso-central and acrostichal bristles being obscured and the chaetotaxy and setation of the anepisternum and katepisternum not being visible (bristles evident in Figure 5).

As far as the visible legs are concerned, there is no evidence of preapical dorsal bristles, and the forefemur does not appear to exhibit the row of short, strong spinules diagnostic for the genus *Curtonotum*. This, however, is probably again due to poor preservation.

The writer has been unable to accurately assess the number of abdominal segments, either from Théobald's original fig. 8 (Figure 3, this paper), or from the digital images of the specimen (Figure 4). Théobald's interpretation of a tubular abdomen clearly holds no taxonomic value, even were such a shape discernable from the fossil, which it is not. The abdomen appears, in fact, to be shortened and robust rather than 'tubular'.

The most significant external morphological structure in determining the correct placement of the fossil at familial and generic level (other than the head discussed above), is the venation and arrangement of bristles along the costa (c) of the wing (*vide* Figure 6). Théobald's original fig. 8 (Figure 3, this paper), illustrates a more-or-less complete pair of wings with an excavated missing section at the posterior apical lobe of the 'upper' wing. The venation is indicated as a series of unstructured lines, clearly unrelated to the actual arrangement on the fossil specimen. Re-examination of the fossil has revealed that the wing is, in fact, folded back upon itself and broken, and that the

costal margin beyond R_1 , which is so critical in determining the presence of conspicuous costal spines, is visible posteriorly rather than anteriorly. There are clearly no spines along the costa, either before or after R_1 . Cells cup, dm and bm are not visible, so it is not possible to ascribe the species to the Curtonotidae based on these characters.

It must be concluded, therefore, that although many external morphological character states are not visible on the specimen, the clear absence of conspicuous spines on the costa precludes the species from placement in *Curtonotum* (as currently defined). As the head and basal section of the wing are not present on the fossil, it is not possible to ascribe it to a family with any degree of certainty. Thus there is no evidence to support Théobald's familial or generic placement within the Curtonotidae. The specimen and species must, therefore, be treated as *insertae sedis*. It can only be hoped that more suitable fossils of the family Curtonotidae come to light in the future (especially amber-preserved specimens) and that they will elucidate our understanding of the evolutionary history of the family.

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Descriptions of final-instar larvae of *Chlorolestes* Sélys (Odonata: Zygoptera; Synlestidae) from southern Africa, with a key to species

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The seven known species of the genus *Chlorolestes* Sélys are endemic to southern Africa, namely: *C. apricans* Wilmot, *C. conspicuus* Sélys, *C. draconicus* Balinsky, *C. elegans* Pinhey, *C. fasciatus* (Burmeister), *C. tessellatus* (Burmeister) and *C. umbratus* Sélys. Final-instar larvae of these seven species are described and figured, based on material from South Africa and Zimbabwe. An identification key, based on characters of the final-instar larvae is provided, and distribution maps are plotted and discussed for species of the genus. The effects of temperature on the rate of larval growth is discussed.

Keywords: Odonata, Synlestidae, southern Africa, larvae, nymphs, immature stages, taxonomy.

INTRODUCTION

The genus *Chlorolestes* Sélys, 1862, is endemic to southern Africa, and is represented by seven known species, which are largely restricted to montane habitats in rivers and streams. The genus is included by Brinck (1955), in what he terms the palaeogenic and palaeo-endemic 'Old Element' of the Afrotropical fauna.

Adults of the southern African species are well documented and good identification keys are available (Pinhey 1951; Tarboton & Tarboton 2005). Larvae are poorly known, however, and the final-instar larvae of the species *C. conspicuus* (Barnard 1921, 1937), *C. elegans* (Pinhey 1958) and *C. fasciatus* (Samways & Whiteley 1997; Samways & Wilmot 2003), have been previously illustrated, but incompletely described. Comparative identification keys to final-instar larvae are not available.

This paper provides detailed descriptions of the final-instar larvae of the seven known species, together with an identification key. Distribution records of the species are also provided based on adult specimens housed in institutional collections and recorded in the literature.

Following Pinhey (1951, 1984), *C. longicaudus* (Burmeister, 1839) is not deemed to have specific status and is included with *C. tessellatus*, which has priority.

MATERIAL AND METHODS

With the exception of *C. elegans* Pinhey, 1950, the description of which is based on that of Pinhey (1958) and a single penultimate instar larva (F1) from the Vumba Mountains, Zimbabwe (National Museum of Zimbabwe, Bulawayo), all material was collected in the field by the writer. Species determinations result from teneral imagines reared in the laboratory. The exuviae of these specimens, together with final-instar larvae collected from sites unique to the particular species as evidenced by the adults present, are used for description.

All material is stored in 70% ethyl alcohol. Permanent mounts using euparal, cleared in 5% potassium hydroxide (KOH) where required, were made of the antenna, prementum, proventriculus, and caudal appendages.

Illustrations were prepared using a binocular microscope with a *camera lucida* attachment. Measurements were taken to the nearest 0.1 mm using a micrometric eye-piece. The following measurements were taken. (Dorsal aspect): total body length (midline from front of head to base of median caudal appendage, including pedicel); head width (widest point across the eyes); antennal length (total of individual segments); prementum length and width (flattened; length on midline from anterior margin to labial suture; width at widest point at base of labial palps); and wing sheaths (midline from anterior margin to apex). (Lateral aspect): caudal appendages (length excluding pedicel along median axis from base to apex; width at widest point). Following Chutter (1961), only entire caudal appendages were measured, i.e. regenerating appendages were excluded.

In order to prevent repetition the final-instar larva of *C. tessellatus* is described in full, with other species of the genus compared to it. The terminology used for the labium follows Corbet (1953), as elaborated on in Samways & Wilmot (2003). It should be noted that 'Albert District' cited by Ris (1921) as a record for *C. fasciatus* is not 'Prince Albert', as interpreted by Barnard (1937), but the historic name of 'Burghersdorp' in the Eastern Cape Province (C.J. Skead pers. comm.).

Distribution maps (Figures 34–38) are based on records provided by Balinsky (1956), Barnard (1937), Brinck (1955), Pinhey (1950, 1951, 1958, 1984), Ris (1921) and Wilmot (1975), and confirmed determinations of adult material housed in: Albany Museum, Grahamstown, South Africa (AMGS); Durban Museum, Durban, South Africa; Nasionale Museum, Bloemfontein, South Africa; Natal Museum, Pietermaritzburg, South Africa; Natural History Museum of London, London, United Kingdom; Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe (NMBZ); Rhodes University, Grahamstown, South Africa; Royal Scottish Museum, Edinburgh, Scotland, United Kingdom; South African Museum, Cape Town, South Africa; Transvaal Museum, Pretoria, South Africa; University of Stellenbosch, Stellenbosch, South Africa; University of the Witwatersrand, Johannesburg, South Africa.

SYSTEMATICS

KEY TO FINAL-INSTAR LARVAE OF *CHOROLESTES* SÉLYS

1. Antennae without ‘wart-like’ structure at bases (as in Figure 14) (except in *C. fasciatus* in which they are only vaguely evident), and pedicel either the longest antennal segment, or equal to each of 1st and 2nd flagellar segments (Figures 20–23); labial palp with intermediate hook toothed distally, end hook with distinct tooth at base above serrations or $\frac{1}{10}$ length of hook, and outer basal angle without dark spot (Figures 27–30); proventriculus with eight major and eight minor folds, all toothed (Figure 7); caudal appendages broad, lamellate with pedicels and dark vertical band half to two-thirds along length (Figure 8 & 9), setae along margins of appendages short and fine except on dorsal edge of median appendage and ventral edges of lateral appendages, where spinulose (Western and Eastern Cape, Lesotho, KwaZulu-Natal, Mpumalanga, North West and Limpopo Provinces, Inyanga Mountains on Zimbabwe/Mozambique border) 2. Subgenus *Euchlorolestes* Barnard
 - Antennae with ‘wart-like’ structure at bases (Figure 13), and pedicel the longest segment of antenna; labial palp with intermediate hook toothed or not toothed distally, and end hook with or without tooth (Figures 31–33); proventriculus with eight major and eight minor folds, with teeth only on major folds (Figure 15); caudal appendages broad, lamellate with pedicels, and colour pattern being either broad vertical band expanded terminally on median axis with dark spots flanking median axis in posterior two-thirds, or being variously mottled, with all margins with spines and spiniform setae or dorsal and ventral margins of both median and lateral appendages with setae not in single row, but multiple and every second one robust (as in Figures 16–17, 18–19) (Western Cape and Eastern Cape Provinces of South Africa) 5. Subgenus *Chlorolestes sensu stricto*
2. Total length (excluding caudal appendages) generally 24–26 mm, but reaching 30 mm in *C. tessellatus*; antenna with scape equal to length of 2nd flagellar segment (Figures 20, 21, 23); end hook of labial palp with basal tooth immediately adjacent to serrations of inner margin (Figures 27, 28, 30) 3
 - Larger species, with total length (excluding caudal appendages) greater than 30 mm; antenna with scape distinctly shorter than 2nd flagellar segment (Figure 22); end hook of labial palp with basal tooth not adjacent to serrations of inner margin, but approximately $\frac{1}{10}$ length of end hook (Figure 29) *C. draconicus* Balinsky
3. Antenna with pedicel, 1st and 2nd flagellar segments approximately equal in length (Figures 20, 21); caudal appendages with distinct, dark vertical band approximately $\frac{2}{3}$ of length (Figure 8 & 9) 4
 - Antenna with pedicel longer than either 1st or 2nd antennal segments; caudal appendages with very broad diffuse brown traverse band centrally placed *C. elegans* Pinhey

4. 'Wart-like' structures at bases of antennae as in *C. conspicuus*; only vaguely evident; anterior margin of prementum with 14–18 serrations to either side of mid-line; labial palps with end hook long, narrow and sharp-pointed, and tooth at base sharp and narrow (Figure 28); abdomen with lateral spines on terga 5(6)–7 feeble, and sharp on terga 8 and 9; cerci in both sexes as in *C. umbratus*, with male long, notched at base on ventral margin, and tapered to a blunt point, and female short with broad base, and dorsal surface excised from $\frac{2}{3}$ of length to give tapered apex *C. fasciatus* (Burmeister)
- 'Wart-like' structures at bases of antennae absent (Figure 14); anterior margin of prementum with 18–20 blunt serrations to either side of mid-line (Figure 4); labial palps with end hook bluntly-pointed (Figures 3, 27); abdomen with distinct lateral spines on terga 6–9; cerci in male long, upcurved, notched at base on ventral margin, and $\frac{1}{3}$ from base tapered to blunt point, and in female short, acutely pointed (Figure 10), and in both sexes curve outward from mid-line of body *C. tessellatus* (Burmeister)
5. Large species with total length (excluding caudal appendages) generally 27–31 mm; antenna with scape 0.6 x length of pedicel, and shorter than each of 1st and 2nd flagellar segments (Figure 24); labium generally subquadrate compared to other species with width 0.8 x length; anterior margin of prementum with no serrations; labial palps with intermediate hook not toothed distally, end hook with no tooth at base, outer basal angle with dark spot, and serrations on median margin less distinct than in other species (Figure 31); caudal appendages broad, lamellate with pedicels, and colour pattern being broad, dark vertical band expanded terminally on median axis with dark spots flanking median axis in posterior $\frac{2}{3}$, all margins with spines and spiniform setae, and median appendage width approximately 0.5 x length and lateral appendages 0.45 x length (Figures 16–17) *C. conspicuus* Sélys
- Small species with total length (excluding caudal appendages) generally 17–22 mm; antenna with scape 0.7 x length of pedicel, and shorter than, or equal to, each of 1st and 2nd flagellar segments; labium with prementum triangular-shaped, flat and elongated with width 0.7 x length, and anterior margin of prementum with blunt serrations; labial palps with intermediate hook toothed or not toothed distally, end hook with or without tooth at base, outer basal angle with or without dark spot, and serrations on median margin of palp rounded and incised as in all other species, except *C. conspicuus*; caudal appendages broad, lamellate with pedicels, and colour pattern variously mottled with dorsal and ventral margins of both median and lateral appendages with setae not in single row, but in multiple rows and every second seta robust, median appendage with width at most 0.45 x length and lateral appendages at most 0.4 x length 6
6. Antenna with scape equal to each of 1st and 2nd flagellar segments (Figure 25); labium with anterior margin of prementum having 16–18 blunt serrations to either side of mid-line, four distinctive brown spots along each lateral margin, and labial palps with

- intermediate hook blunt and not toothed distally, end hook without tooth at base, and outer basal angle with dark spot (Figure 32); legs with two dark bands on tibiae and three on femora; abdomen with sharp lateral spines on terga 5–9; caudal appendages having colour pattern of brown band along mid-line and 10 (5 dorsal and 5 ventral) dark brown areas on outer margins, and width: length ratios of 0.45 for median appendage and 0.4 for lateral appendages (Figures 18 & 19) *C. umbratus* Sélys
- Antenna with scape shorter than each of 1st and 2nd flagellar segments (Figure 26); labium with anterior margin of prementum having 12–14 blunt serrations to either side of mid-line, lateral margins uniform in colour, and labial palps with intermediate hook angled and toothed distally, end hook with or without tooth at base (Figure 33), outer basal angle uniform in colour; legs with two dark bands on both tibiae and femora; abdomen with sharp lateral spines on terga (6) 7–9; caudal appendages with colour pattern as above, but generally paler and less well defined, and width:length ratios of only 0.35 for median appendage and 0.3 for lateral appendages *C. apricans* Wilmot

NEW DESCRIPTIONS OF FINAL INSTAR LARVAE

GENUS: *CHLOROLESTES* SÉLYS, 1862

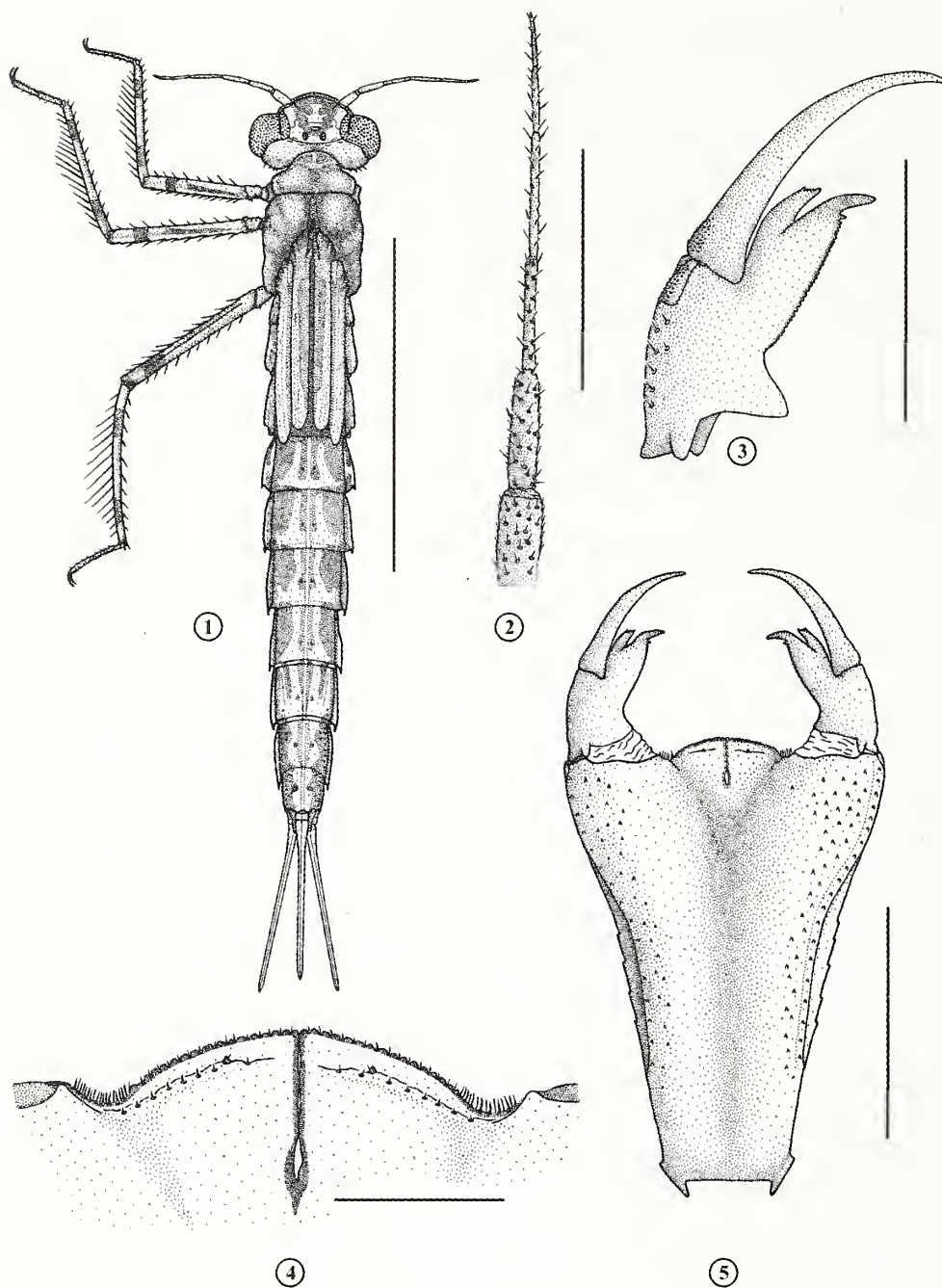
Type species: *Chlorolestes conspicuus* Sélys, 1862: 32

Chlorolestes apricans Wilmot, 1975: 13

Figures 26, 33 & 38

MATERIAL EXAMINED: 1♂, South Africa: Eastern Cape, Post Retief, Koonap River, 32°27'55"S, 26°30'55"E, 20.xi.1981, B.C. Wilmot; 1♀, same except: 1.xii.1981; 1♀ exuviae, same except: xii.1981 (AMGS).

DESCRIPTION: Head: Antenna as in *C. tessellatus*; generally slender in appearance, with scape, pedicel and five-segmented flagellum (Figure 26). Scape 0.7 (range: 0.7–0.7; $n=3$) x length of pedicel; pedicel longer than each of 1st and 2nd flagellar segments, and flagellum 0.6 (range: 0.6–0.6; $n=3$) x total length of antenna. ‘Wart-like’ structure at bases of antennae as in *C. conspicuus* and *C. umbratus*. Labium with prementum, similar to all other species of the genus, except *C. conspicuus*; triangular-shaped and tapered, with width 0.7 (range: 0.7–0.7; $n=3$) x length. Anterior margin of prementum similar to *C. tessellatus*, but with 12–14 blunt serrations, with spiniform setae between, to either side of mid-line; lateral to these >10 piliform setae tightly spaced at base of each labial palp. Median lobe similar to *C. conspicuus* and *C. umbratus*, with single tooth and small



Figures 1–5. *Chlorolestes tessellatus* (Burmeister), final-instar larva. 1, larval habitus, dorsal aspect (excluding right legs); 2, antenna; 3, labial palp, left dorsal aspect; 4, anterior margin of prementum, dorsal aspect; 5, prementum with labial palps, dorsal aspect. Scale bars: 1 = 10 mm; 2 = 2 mm; 3 = 1 mm; 4 = 0.5 mm; 5 = 2 mm.

seta at base to either side of mid-line, and small setae more densely scattered than in *C. tessellatus*. Labial palps as in *C. tessellatus*, with long movable hook, but intermediate hook angled and toothed distally and end hook steeply inclined, with or without tooth at base (Figure 33). Serrations on median margin of palps rounded and incised as in all other species, except *C. conspicuus*. Mandibles, eyes and ocelli as in all other species of the genus (*vide C. tessellatus*).

Thorax: Proventriculus as in *C. conspicuus* with 2–4 teeth on each major fold.

Wing sheaths: All parallel with mesothoracic sheath to $\frac{3}{4}$ distance across 3rd tergum, and metathoracic sheath to approximately posterior margin of 3rd tergum.

Legs: As in *C. tessellatus*, with two dark bands on both femur and tibia of all legs.

Abdomen: Sharp lateral spines on terga (6) 7–9; cerci in ♂ 2 x length of ♀, tapering and slightly upcurved terminally; ♀ short, tapering and wedge-shaped terminally, as in *C. umbratus*.

Genitalia: As in all other species of the genus (*vide C. tessellatus*).

Caudal appendages: Broad, lamellate with pedicels; colour pattern comprising brown band along mid-line and 10 (5 dorsal and 5 ventral), dark brown areas on outer margins of both median and lateral appendages. In this regard, similar to *C. umbratus*, but generally paler and thus less well defined. As in *C. umbratus*, dorsal and ventral margin of both median and lateral appendages with setae not in single row, but multiple and every second one robust. Narrowest of all species, including *C. umbratus*; median appendage with width only 0.35 x length and lateral appendages only 0.3 x length.

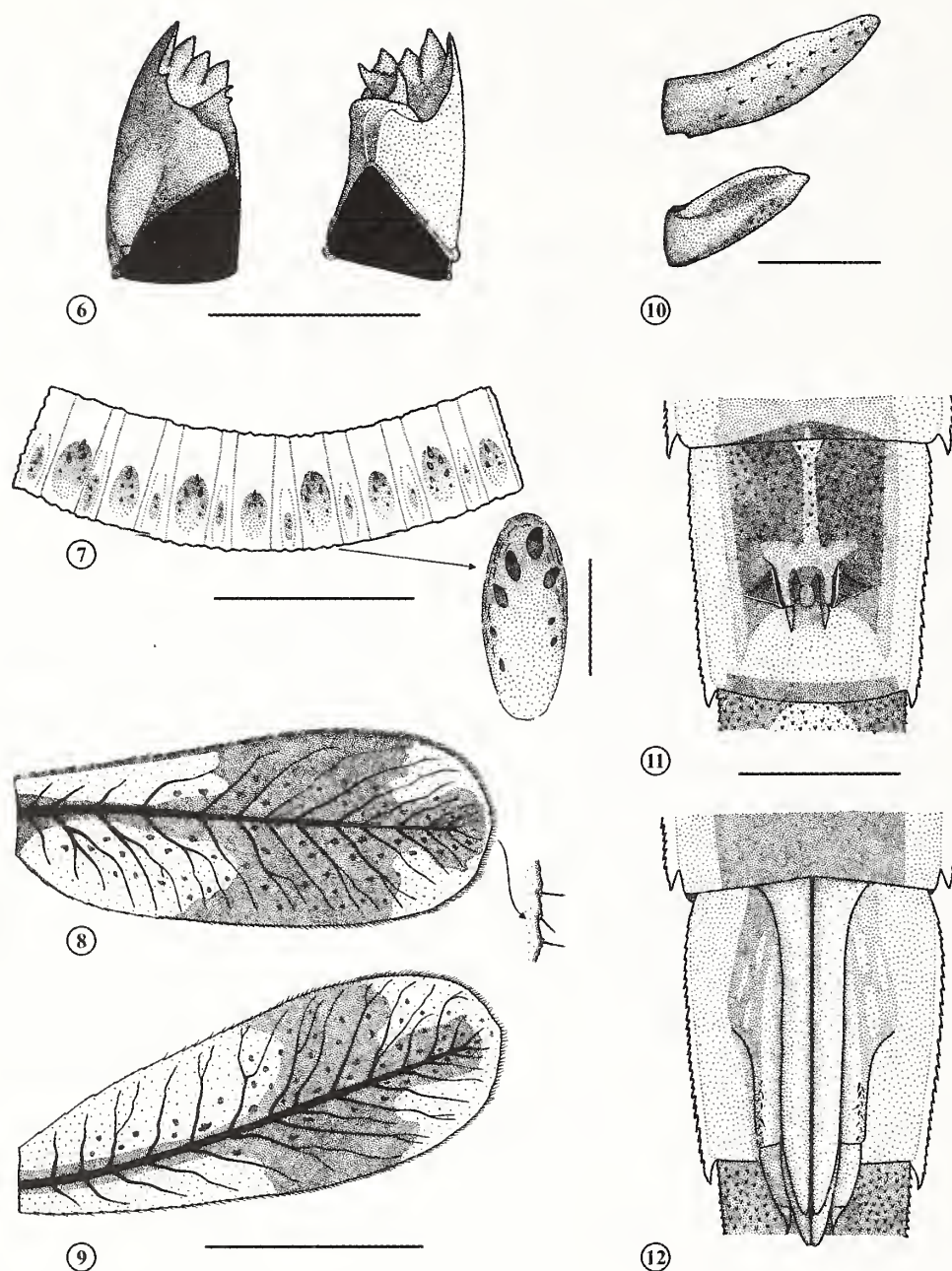
DIAGNOSIS: Generally as in *C. tessellatus*, but much smaller and comparable to *C. umbratus*. Dorsal surface of head with pattern similar to *C. tessellatus*; dorsum of terga 1–3 generally pale, terga 4–8 with central parts generally dark brown, with pale median stripe and a second curved stripe to either side, and terga 9 and 10 with expanded pale area. Lateral keels as in *C. umbratus*.

DISTRIBUTION: Restricted to the Winterberg/Amathole Mountains of the Eastern Cape Province (Figure 38).

Chlorolestes conspicuus Sélys, 1862: 32

Figures 13, 15–17, 24, 31 & 37

MATERIAL EXAMINED: 1♂, 2♀, South Africa: Western Cape, Table Mountain, Orange Kloof, 33°59'50"S, 18°23'45"E, 26.i.1976, B.C. Wilmot; 4♂; 1♂ exuviae, same except:



Figures 6–12. *Chlorolestes tessellatus* (Burmeister), final-instar larva. 6, mandibles; 7, proven-triculus, flattened internal aspect, with enlargement of one major fold (arrowed); 8, median appendage, lateral aspect: with enlargement of marginal setae (arrowed); 9, lateral appendage; 10, cerci, lateral aspect: ♂ (above); ♀ (below); 11, external genitalia: ♂; 12, external genitalia ♀ (below). Scale bars: 6 = 0.5 mm; 7 = 1 mm; 8–9 = 2 mm; 10 = 0.5 mm; 11–12 = 1 mm.

27.i.1976; 4♀, Western Cape, Franschhoek Pass, 33°54'05"S, 19°09'30"E, 30.i.1976, B.C. Wilmot; 2♂, 1♀, Mitchell's Pass, 33°23'30"S, 19°17'00"E, 4.ii.1976, B.C. Wilmot; 3♂, 2♀, Jonkershoek, 33°59'25"S, 18°58'05"E, 3.ii.1976, B.C. Wilmot (AMGS).

DESCRIPTION: Head: Antenna as in *C. tessellatus*; generally slender in appearance with scape, pedicel and five-segmented flagellum (Figure 24). Scape 0.6 (range: 0.6–0.7; $n=20$) x length of pedicel, which is longer than each of 1st and 2nd flagellar segments; and flagellum 0.6 (range: 0.5–0.6; $n=20$) x total length of antenna. 'Wart-like' structure at bases of antennae as in *C. apricans* and *C. umbratus* (Figure 13). Labium generally subquadrate as compared to other species, with width 0.8 (range: 0.8–0.8; $n=20$) x length, and extending posteriorly to the bases of mesothoracic sheath legs. Anterior margin of prementum without serration, only spiniform setae to either side of mid-line, and lateral to these >10 tightly spaced piliform setae at base of each labial palp. On median lobe a single tooth with seta at base to either side of mid-line as in *C. tessellatus*, but small setae more densely scattered. Labial palps as in *C. tessellatus*, except intermediate hook not toothed distally, end hook blunt and robust with no tooth at base, and outer basal angle with dark spot (Figure 31). Serrations on median margin of palps less distinct than in other species. Mandibles, eyes and ocelli as in all other species (*vide C. tessellatus*).

Thorax: Proventriculus with eight major and eight minor folds, with teeth only on major folds; 2–3 teeth on each major fold, with those on alternating major folds slightly smaller (Figure 15).

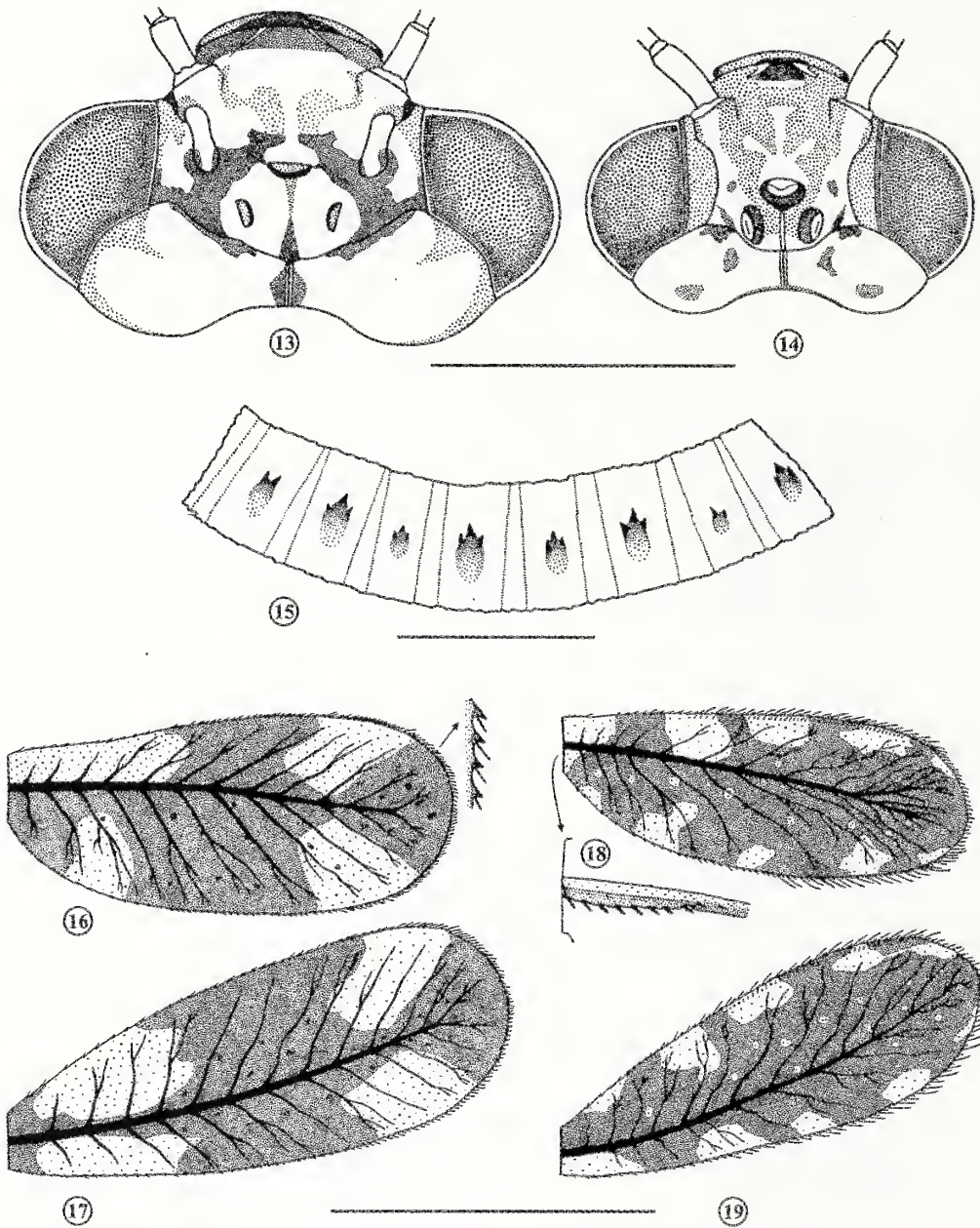
Wing sheaths: As in *C. tessellatus*, parallel with mesothoracic sheath to just short of posterior margin of 3rd tergum, and metathoracic sheath to just beyond this margin.

Legs: As in *C. tessellatus*, but on tibiae two brown-grey to black bands and three on femora; basal one on prothoracic femora faint/pale.

Abdomen: Sharp lateral spines on terga (5) 6–9; cerci in ♂, long, up-curved, dorsal edge with thickening midway along length, then tapering to a point; ♀ short, simple, and wedge-shaped.

Genitalia: As in all other species of the genus (*vide C. tessellatus*).

Caudal appendages: Distinctly broader, i.e. deeper than in other species; dark vertical band wider than in *C. tessellatus* and clearly expanded terminally on median axis; dark spots flanking median axis in posterior $\frac{2}{3}$ only; median axis expanded laterally for less than $\frac{1}{3}$ of length from base; all margins with spines and spiniform setae; median appendage width approximately 0.5 x length, and lateral appendages 0.45 x length (Figures 16 & 17).



Figures 13–19. *Chlorolestes* spp. final-instar larvae. 13, *C. conspicuus* Sélys, head, dorsal aspect; 14, *C. tessellatus* (Burmeister), head, dorsal aspect; 15, *C. conspicuus* Sélys, proventriculus, flattened interior aspect; 16, *C. conspicuus* Sélys, caudal appendage, lateral aspect; median appendage with enlargement of marginal spines and spiniform setae (arrowed); 17, *C. conspicuus* Sélys, lateral appendage; 18, *C. umbratus* Sélys, caudal appendage, lateral aspect; median appendage with enlargement of basal, lateral expansion of median axis (arrowed); 19, *C. umbratus* Sélys, lateral appendage. Scale bars: 13–14, 16–19 = 3 mm; 15 = 1 mm.

DIAGNOSIS: Generally as in *C. tessellatus*, except head with obvious dark ring around each ocellus and pale between ocelli (Figure 13), and abdomen darker than in *C. tessellatus* with terga mostly dark brown and lateral keels pale coloured.

DISTRIBUTION: Restricted to the southern region of the Western Cape Province (Figure 37).

Chlorolestes draconicus Balinsky, 1956: 511

Figures 22, 29 & 38

MATERIAL EXAMINED: 1♂, 4♂ exuviae, 1♀ exuviae, South Africa: KwaZulu-Natal, Royal Natal National Park, Mahai River, 28°41'10"S, 28°55'50"E, 12.xii.1974, B.C. Wilmot (AMGS).

DESCRIPTION: Head: Antenna as in *C. tessellatus*; generally slender in appearance with scape, pedicel and five-segmented flagellum (Figure 22). Scape 0.7 (range: 0.7–0.8; $n=6$) x length of pedicel, and equal to length of 2nd flagellar segment; pedicel longer than each of 1st and 2nd flagellar segments; and flagellum 0.6 (range: 0.6–0.6; $n=6$) x total length of antenna. No ‘wart-like’ structures at bases of antennae. Labium with prementum triangular-shaped, flat and elongated, as in *C. tessellatus*, with width 0.7 (range: 0.7–0.7; $n=20$) x length; anterior margin of prementum as in *C. tessellatus*, except with approximately 12–14 blunt serrations, followed by 2–4 spiniform setae to either side of mid-line, and then >10 piliform setae tightly spaced at base of each labial palp; lateral to these with approximately 10 piliform setae at base of each lateral lobe. Median lobe as in *C. tessellatus*. Labial palps as in *C. tessellatus*, but end hook with broader base and sharp point; associated tooth not in contact with serrated inner margin, but approximately $\frac{1}{10}$ length of end hook (Figure 29). Mandibles, eyes and ocelli as in all other species of the genus (*vide C. tessellatus*).

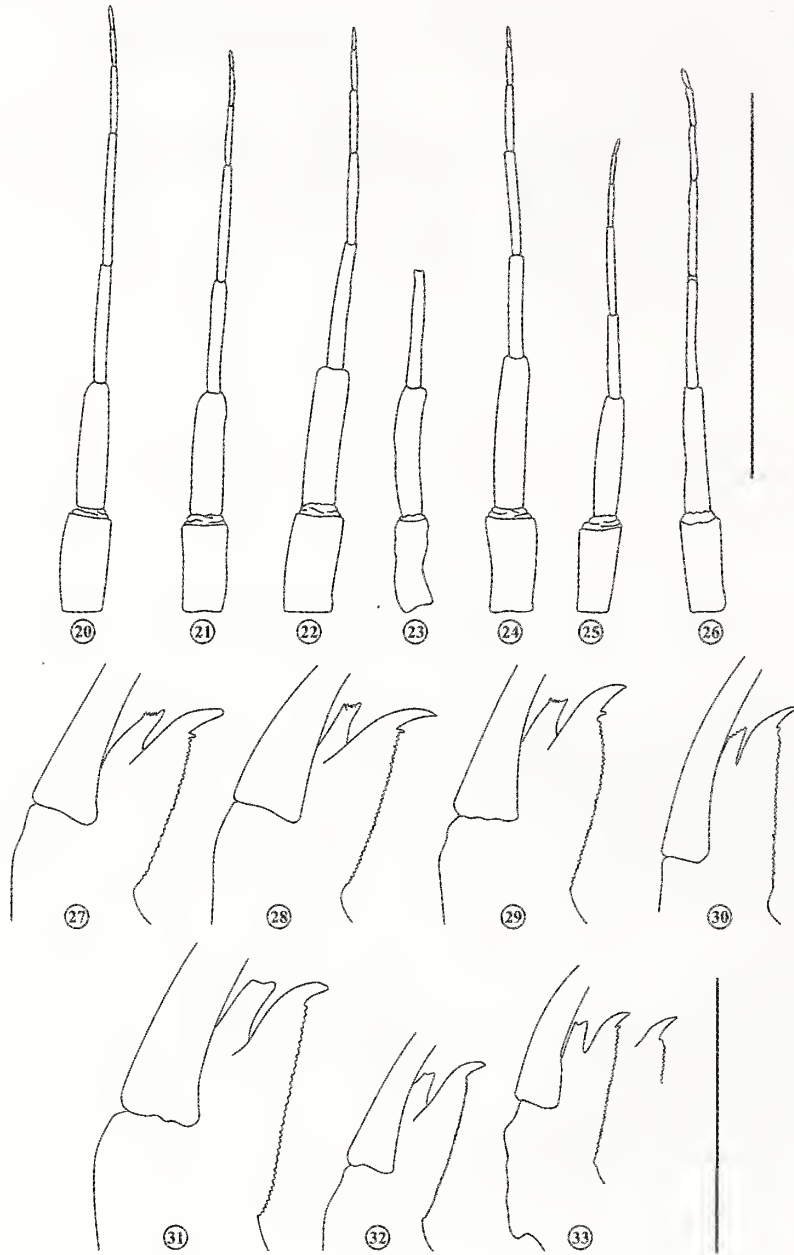
Thorax: Proventriculus as in *C. tessellatus*.

Wing sheaths: All parallel with mesothoracic sheath to just short of, or at posterior margin of 3rd tergum, and metathoracic sheath to just beyond this margin.

Legs: As in *C. tessellatus*.

Abdomen: Lateral spines on 5th tergum very small, and distinct on terga 8 and 9; cerci of ♂ long, similar to *C. fasciatus*; ♀ short, broad with down-turned blunt point.

Genitalia: As in other species of the genus (*vide C. tessellatus*).



Figures 20–26. *Chlorolestes* spp. final-instar larvae, antenna. **20**, *C. tessellatus* (Burmeister); **21**, *C. fasciatus* (Burmeister); **22**, *C. draconicus* Balinsky; **23**, *C. elegans* Pinhey (only scape, pedicel and 1st flagellar segments of penultimate instar); **24**, *C. conspicuus* Sélys; **25**, *C. umbratus* Sélys; **26**, *C. apricans* Wilmot. **Figures 27–33.** *Chlorolestes* spp. final-instar larvae, labial palp. **27**, *C. tessellatus*; **28**, *C. fasciatus*; **29**, *C. draconicus*; **30**, *C. elegans* (penultimate instar); **31**, *C. conspicuus*; **32**, *C. umbratus*; **33**, *C. apricans* (end hook shown with and without basal tooth). Scale bars: 20–26 = 3 mm; 27–33 = 1 mm.

Caudal appendages: As for *C. elegans*, *C. fasciatus* and *C. tessellatus*, with setae along margins of appendages short and fine, except on dorsal edge of median appendage and ventral edges of lateral appendages, where spinulose; median appendage with width approximately 0.4 x length, and lateral appendages marginally less so.

DIAGNOSIS: As in *C. tessellatus*, except dorsal abdominal colour more uniform, similar to *C. conspicuus*.

DISTRIBUTION: Restricted to high altitudes in the Natal Drakensberg Mountains (Figure 38).

Chlorolestes elegans Pinhey, 1950: 260

Figures 23, 30 & 38

MATERIAL EXAMINED: 1♂ (penultimate instar), Zimbabwe, Vumba Mountains, 19°07'S, 32°44'E, xi.1956, E.C.G. Pinhey (NMBZ).

DESCRIPTION: Head: Antenna as in *C. tessellatus*; generally slender in appearance, with scape, pedicel and five-segmented flagellum (Figure 23). Scape approximately 0.7 x length of pedicel, which is longer than each of 1st and 2nd flagellar segments. No 'wart-like' structures at bases of antennae. Labium with prementum triangular-shaped, flat and elongated, as in *C. tessellatus*, with width 0.7 ($n=1$) x length; anterior margin of prementum as in *C. tessellatus*, but with approximately 16–18 blunt serrations, each with spatulate seta to either side of mid-line, and lateral to these >10 spiniform, not piliiform, setae tightly spaced at base of each labial palp. Median lobe as in *C. tessellatus*. Labial palps as in *C. tessellatus*, with end hook blunt and robust and associated tooth immediately at base (Figure 30). Mandibles, eyes and ocelli as in all other species of the genus (*vide C. tessellatus*).

Thorax: Proventriculus as in *C. tessellatus*.

Wing sheaths: All parallel with mesothoracic sheath to posterior margin of 3rd tergum, and metathoracic sheath to $\frac{1}{3}$ distance across 4th tergum; colour pattern of legs unknown (single available specimen badly bleached).

Abdomen: Lateral spines on terga (5) 6–9; cerci of ♂ bent up at $\frac{1}{3}$ from base, then tapering to blunt point; ♀ no data.

Genitalia: As in all other species of the genus (*vide C. tessellatus*).

Caudal appendages: Simple, lamellate, yellowish, with very broad diffuse brown traverse band centrally placed (Pinhey 1958); median axis expanded laterally for less

than $\frac{1}{3}$ of length from base; as in *C. draconicus*, *C. fasciatus* and *C. tessellatus*, with setae along margins of appendages short and fine, except on dorsal edge of median appendage and ventral edges of lateral appendages, where spinulose; median appendage with width approximately 0.4 x length, and lateral appendages marginally less so.

DIAGNOSIS: As in *C. tessellatus*, but the largest of the known species.

DISTRIBUTION: Only recorded from the Mpumalanga and Limpopo Provinces of South Africa, and the Inyanga Mountains on the Zimbabwe/Mozambique border (Figure 38).

Chlorolestes fasciatus (Burmeister, 1839: 36)

Figures 21, 28 & 36

MATERIAL EXAMINED: 3♂, 2♀, South Africa: KwaZulu-Natal, Drakensberg Gardens, 29°45'30"S, 29°13'50"E, 15.i.1974, B.C. Wilmot; 4♂, 1♂ exuviae, 1♀, 2♀ exuviae, KwaZulu-Natal, Royal Natal National Park, 28°41'10"S, 28°55'50"E, 10.xii.1974, B.C. Wilmot; 1♂ exuviae, 2♀ exuviae, same except: 12.xii.1974. 5♂, 2♀, Free State, Golden Gate National Park, 28°30'40"S, 28°30'40"E, x.1974, B.C. Wilmot; 2♂, 2♀, Eastern Cape, Amathole Mountains, Hogsback, 32°34'45"S, 26°56'10"E, 20.xi.1974, B.C. Wilmot (AMGS).

DESCRIPTION: Head: Antennae as in *C. tessellatus*; generally slender in appearance, with scape, pedicel and five-segmented flagellum (Figure 21). Scape 0.7 (range: 0.7–0.8; $n=27$) x length of pedicel; pedicel with 1st and 2nd flagellar segments approximately equal in length; flagellum approximately 0.6 (range: 0.6–0.7; $n=26$) x total length of antenna. ‘Wart-like’ structures at bases of antennae present, but unlike *C. apricans*, *C. conspicuus*, and *C. umbratus*, only vaguely evident. Labium with prementum triangular-shaped, flat and elongated, as in *C. tessellatus*, with width 0.7 (range: 0.7–0.7; $n=27$) x length; anterior margin and median lobe of prementum also as for *C. tessellatus*, except on anterior margin with less blunt serrations, being 14–18 either side of mid-line, and then >10 piliform setae tightly spaced at base of each labial palp. Labial palps as in *C. tessellatus*, except end hook slightly longer, narrower and sharp-pointed, with tooth at base sharp and narrow (Figure 28). Mandibles, eyes and ocelli as in all other species of the genus (*vide C. tessellatus*).

Thorax: Proventriculus as in *C. tessellatus*.

Wings sheaths: As in *C. tessellatus*, i.e. parallel with mesothoracic sheath to just short of posterior margin of 3rd tergum, and metathoracic to just beyond this margin; legs also as in *C. tessellatus*.

Abdomen: Lateral spines on terga 5(6)–7 feeble, and sharp on terga 8 and 9. Cerci in ♂ long, notched at base on ventral margin, and tapering to a blunt point; ♀ short, with broad base and dorsal surface excised from $\frac{2}{3}$ of length to tapered apex. Cerci in both sexes as in *C. umbratus*.

Genitalia: As in all other species of the genus (*vide C. tessellatus*).

Caudal appendages: As in *C. draconicus* and *C. tessellatus*; setae along margins of appendages short and fine, except on dorsal edge of median appendage and ventral edges of lateral appendages, where they are spinulose; median appendage with width approximately 0.4 x length, and lateral appendages marginally less so.

DIAGNOSIS: As in *C. tessellatus*; colour differences, if any, extremely difficult to distinguish.

DISTRIBUTION: Most frequently recorded on high altitude grassland streams, from the Eastern Cape Province through Lesotho, Free State, KwaZulu-Natal, and Swaziland to Mpumalanga, Gauteng, and North West and Limpopo Provinces (Figure 36).

Chlorolestes tessellatus (Burmeister, 1839: 35)

Figures 1–5, 6–12, 14, 20, 27 & 35

MATERIAL EXAMINED: 2♂, 1♂ exuviae, 4♀, 1♀ exuviae, South Africa: Eastern Cape, Amathole Mountains, Hogsback Inn, 32°35'45"S, 26°56'25"E, 14.xii.1971, B.C. Wilmot; 1♂, 5♀, same except: 23.xii.1971; 1♂, 3♀, same except: 18.iii.1972; 4♂, 1♀, same except: 17.xii.1972; 6♂, 9♀, same except: 29.xi.1973; 15♂, 13♀, same except: 13.ii.1974; 6♂, 3♀, Eastern Cape, Bloukrans River, Oak Valley, 33°19'15"S, 26°36'10"E, 17.i.1973, B.C. Wilmot; 7♂, 2♀, same except: 18.ix.1973; 7♂, 3♀, same except: 18.x.1973; 8♂, 7♀, same except: 21.xii.1973; 3♂, 3♀, same except: 15.i.1975 (AMGS).

DESCRIPTION: Head: Antenna slender, with scape, pedicel and five-segmented flagellum (Figures 2, 20). Scape 0.7 (*range*: 0.7–0.9; *n*=110) x length of pedicel; pedicel with 1st and 2nd flagellar segments almost equal in length; flagellum 0.6 (*range*: 0.6–0.7; *n*=110) x total length of antenna. No ‘wart-like’ structures at bases of antennae (Figure 14). Labium with prementum triangular-shaped, flat and elongated with width 0.7 (*range*: 0.7–0.8; *n*=113) x length (Figure 5); anterior margin with median cleft shallowly incised and almost closed and approximately 18–20 blunt serrations, each with spiniform seta to either side of mid-line; lateral to these >10 piliform setae tightly spaced at base of each labial palp (Figure 4). One tooth on median lobe, with small seta at base and small

setae thinly scattered to either side of mid-line. Setae conspicuous on lateral margins and dorsal surface immediately adjacent to these margins, except in basal quarter. Labial palps with distinctly curved, long movable hook, peg-like intermediate hook toothed distally, and bluntly-pointed end hook, with distinct tooth at base (Figures 3, 20). Inner margins of palps with serrations rounded and incised. Mandibles asymmetrical; left mandible with second row of teeth, and right with hook-like process posterior to main edge of four teeth (Figure 6). Eyes in mature larvae very large, as development of adult eyes beneath cuticle extends ommatidial surface medially to bases of antennae. Three clearly-defined ocelli present.

Thorax: Proventriculus with eight major and eight minor folds, all with teeth facing anteriorly towards oesophagus. Major folds normally each with 3–5 large teeth and a similar number of small teeth posterior to them; minor folds each with 1–4 teeth (Figure 7).

Wing sheaths: All parallel; mesothoracic sheath reaching to just short of posterior margin of 3rd tergum, and metathoracic sheath, to just beyond this margin (Figure 1). In specimens close to emergence wing sheaths are divergent, and venation of wings obvious beneath the cuticle.

Legs: With two bands of dark brown to grey-black on femur and tibia of all legs. Short spines along dorsal and ventral edges of femora, ventral edge of tibiae, and dorsal surface of tarsi; dorsal (outer) edges of tibiae with long setae and ventral surfaces of tarsi with feathered setae.

Abdomen: Segments keeled laterally, with distinct lateral spines on terga 6–9. Cerci in ♂ long, upcurved, notched at base on ventral margin, and $\frac{1}{3}$ from base tapered to blunt point; ♀ short, acutely pointed (Figure 10); in both sexes curve outward from mid-line of body.

Genitalia: ♂ simple, with only single pair of gonopophyses either side of gonopore; ♀ with three pairs of gonopophyses (valvulae), large, extending beyond posterior margin of 9th abdominal sternum with first pair 1.2 x length of 9th abdominal sternum (Figure 11 & 12).

Caudal appendages: broad, lamellate, with pedicels and dark vertical band approximately two-thirds along length (Figure 8 & 9). Median axis expanded laterally, in basal quarter with teeth, and secondary tracheae obvious and oblique to main axis. Setae along margins of appendages short and fine, except on dorsal edge of median appendage and ventral edges of lateral appendages where spinulose. Median appendage with width approximately 0.4 x length, and lateral appendages marginally less so.

DIAGNOSIS: General appearance, long, slender and tapering, with caudal lamellae (Figure 1); head rounded with dark brown median band anterior of ocelli (Figure 14); thorax narrower than head; abdomen comprising ten segments, with dorsal pattern of

Table 1. Comparative measurements of final-instar larvae of *Chlorolestes tessellatus* (Burmeister) from two localities in the Eastern Cape, South Africa (*mean* followed by *range* in brackets, all in millimeters). Elevations: Hogsback (1 180 m.a.s.l.); Oak Valley (440 m.a.s.l.).

Measurements	Hogsback (Nov.–Dec.) (<i>n</i> =32, unless otherwise stated)	Hogsback (Feb.–Mar.) (<i>n</i> =32)	Oak Valley (Sept.–Nov.) (<i>n</i> =19, unless otherwise stated)	Oak Valley (Dec.–Jan.) (<i>n</i> =30)
Total length (excl. caudal appendages)	26.1 (23.0–30.0)	22.6 (18.5–30.0)	25.8 (24.0–28.5)	23.8 (21.0–27.8)
Head width	4.4 (4.2–4.7)	4.1 (3.9–4.5)	4.2 (4.0–4.5)	4.0 (3.7–4.1)
Antenna length (total)	5.0 (4.6–5.4); <i>n</i> =30	4.6 (4.2–5.3)	5.0 (4.6–5.6); <i>n</i> =18	4.9 (4.6–5.4)
Flagellum length	3.1 (2.9–3.5); <i>n</i> =30	2.9 (2.6–3.4)	3.2 (2.8–3.7); <i>n</i> =18	3.2 (2.8–3.6)
Premontum length	3.9 (3.8–4.2)	3.7 (3.4–3.9)	3.7 (3.5–3.9)	3.6 (3.3–3.9)
Premontum width	2.9 (2.7–3.0)	2.7 (2.6–2.9)	2.7 (2.5–2.8)	2.5 (2.3–2.7)
Wing sheaths length				
Mesothoracic sheath	6.4 (5.9–7.2)	6.0 (5.5–6.6)	6.3 (5.9–6.9)	5.9 (5.5–6.3)
Metathoracic sheath	5.9 (5.3–6.5)	5.6 (5.1–6.1)	5.8 (5.4–6.2)	5.5 (4.9–5.7)
Caudal appendages				
Median length	4.8 (4.3–5.4)	4.3 (3.7–5.0)	4.8 (4.6–5.3)	4.6 (4.1–5.0)
Median width	1.8 (1.6–2.1)	1.7 (1.5–1.9)	1.9 (1.7–2.0)	1.8 (1.5–2.1)
Lateral length	5.2 (4.8–5.8)	4.7 (4.1–5.5)	5.2 (4.9–5.7)	4.9 (4.3–5.4)
Lateral width	1.9 (1.7–2.1)	1.7 (1.5–1.9)	1.9 (1.7–2.0)	1.9 (1.7–2.0)

pigmentation as illustrated; colour variable, from pale brown on cream, black-brown on pale brown, to grey-black on light grey; ventral surface uniform white to brown. Lateral keels mostly pale brown or cream in colour.

DISTRIBUTION: Generally recorded from lower altitude woodland streams and rivers, from the Western Cape Province north through the Eastern Cape, KwaZulu-Natal, and Mpumalanga to Gauteng, North West and Limpopo Provinces (Figure 35).

Chlorolestes umbratus Sélys, 1862: 37

Figures 18, 19, 25, 32 & 38

MATERIAL EXAMINED: 1♂ exuviae, 1♀, South Africa: Western Cape, Bloukrans Pass, 33°56'55"S, 23°37'00"E, 29.vii.1970, B.C. Wilmot; 1♂ exuviae, 2♀, 1♀ exuviae, Kaaman's River, 33°57'35"S, 22°32'20"E, x.1970, B.C. Wilmot; 4♂ exuviae, 2♀

exuviae, Jonkershoek Weir, 33°59'25"S, 18°58'05"E, 3.ii.1976, B.C. Wilmot; 1♂ exuviae, Garcia Forestry Station, 34°01'40"S, 21°13'25"E, 9.ii. 1976, B.C. Wilmot; 1♂ exuviae, Bloukrans Pass, 33°56'55"S, 23°37'00"E, 10.ii.1976, B.C. Wilmot (AMGS).

DESCRIPTION: Head: Antenna as in *C. tessellatus*; generally slender in appearance with scape, pedicel and five-segmented flagellum (Figure 25). Scape 0.7 (range: 0.7–0.7; $n=14$) x length of pedicel, and equal to each of 1st and 2nd flagellar segments; pedicel longer than each of 1st and 2nd flagellar segments; and flagellum 0.6 (range: 0.5–0.6; $n=10$) x total length of antenna. Scape brown in colour; proximal $\frac{3}{4}$ of pedicel, all of 1st, 2nd and 3rd flagellar segments, and first half of 4th segment dark brown; terminal segment pale brown. 'Wart-like' structure at bases of antennae as in *C. apricans* and *C. conspicuus*. Labium with prementum triangular-shaped, flat and elongated, as in *C. tessellatus*, with width 0.7 (range: 0.7–0.7; $n=13$) x length. Anterior margin of prementum similar to *C. tessellatus*, but with 16–18 blunt serrations to either side of mid-line, and lateral to these >10 piliform setae tightly spaced at base of each labial palp. Median lobe similar to *C. tessellatus*, with single tooth to either side of mid-line, but similar to *C. conspicuus*, in having more densely scattered small setae. Four distinctive brown spots along each lateral margin of prementum. Labial palps as in *C. tessellatus* with long movable hook, but intermediate hook blunt and not toothed distally, and end hook steeply inclined with no tooth at base (Figure 32). Serrations on median margin rounded and incised as in all other species, except *C. conspicuus*. Similar to *C. conspicuus* with dark spot on outer basal angle of palp. Mandibles, eyes and ocelli as in all other species (*vide C. tessellatus*).

Thorax: Proventriculus as in *C. conspicuus*.

Wing sheaths: All parallel with mesothoracic sheath only to half distance across 3rd tergum, and metathoracic sheath to approximately posterior margin of 3rd tergum.

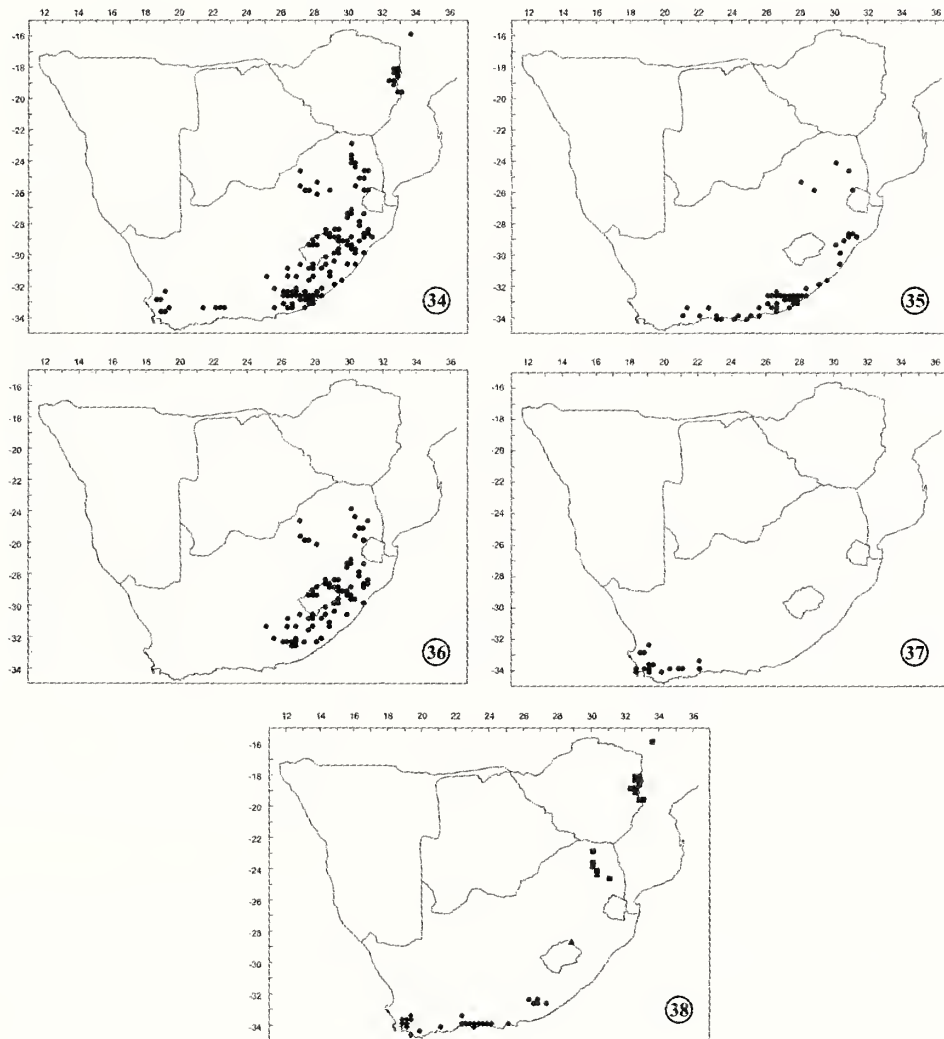
Legs: As in *C. conspicuus*, with two dark bands on tibiae and three on femora.

Abdomen: Sharp lateral spines on terga 5–9; cerci in ♂ long, upcurved tapering to bluntish point with notch at base of ventral margin; ♀ short, tapering and wedge-shaped terminally.

Genitalia: As in all other species of the genus (*vide C. tessellatus*).

Caudal appendages: Broad, lamellate with pedicels, and brown/dark brown in colour, except for five pale areas along dorsal and ventral margins and pale spots flanking median axis (Figures 18 & 19). As in *C. apricans*, dorsal and ventral margin of both median and lateral appendages with setae not in single row, but multiple and every second one robust. Median axis expanded laterally as in *C. tessellatus*. Median appendage with width approximately 0.45 x length and lateral appendages 0.4 x length.

DIAGNOSIS: Generally as in *C. tessellatus*, but much smaller, comparable with *C. apricans*. Dorsal surface of head with pattern similar to *C. tessellatus*; dorsum of abdomen with lateral spines having anterior half and posterior margins dark brown, central portion similar to *C. conspicuus*, but with lateral bands narrower and with dark, narrow band to either side of mid-line to just over mid-length of terga. Lateral keels with anterior half and posterior margin dark brown.



Figures 34–38. Distribution of southern African species of *Chlorolestes* Selys. 34, Coverage of records for *Chlorolestes* Selys; 35, *C. tessellatus* (Burmeister); 36, *C. fasciatus* (Burmeister); 37, *C. conspicuus* Selys; 38, *C. apricans* Wilmot (circle), *C. draconicus* Balinsky (triangle), *C. elegans* Pinhey (square), *C. umbratus* Selys (lozenge).

DISTRIBUTION: Restricted to the southern region of the Western Cape Province and western coastal region of the Eastern Cape Province (Figure 38).

DISCUSSION

The two subgenera, *Chlorolestes sensu stricto* and *Euchlorolestes*, erected by Barnard (1937) after Kennedy (1920) and reaffirmed by Pinhey (1951, 1962), are based on adult characters alone. Examination of the final-instar larvae, particularly characters of the proventriculus and caudal appendages, confirm such a subgeneric division. The final-instar larvae of *Chlorolestes sensu stricto*, comprising *C. apricans*, *C. conspicuus* and *C. umbratus* have the proventriculus with teeth only on the major folds, and caudal appendages with either a broad, dark vertical band expanded terminally on the median axis, with dark spots flanking the median axis in the posterior $\frac{2}{3}$, or variously mottled. Those of *Euchlorolestes*, comprising *C. draconicus*, *C. elegans*, *C. fasciatus* and *C. tessellatus* have the proventriculus with teeth on both the major and minor folds, and the caudal appendages with only a dark vertical band $\frac{1}{2}$ to $\frac{2}{3}$ along the length.

With regard to the final-instar larvae, inter-specific differences within each of the two subgenera are difficult to discern in some instances. For this reason attention is drawn to the known geographical distribution of the species (Figures 34–38). While some of the species are widely separated geographically, several species do overlap in their distribution, and of these the most difficult to separate are *C. fasciatus* and *C. tessellatus*, given their common size range and many shared attributes. Generally, *C. tessellatus* is most commonly found in lower elevation woodland streams and rivers and *C. fasciatus* in high elevation grassland streams, but they are known from common localities in montane areas of the Eastern Cape Province, KwaZulu-Natal, Mpumalanga, and the North West and Limpopo Provinces.

The influence of temperature on the growth of odonate larvae, and thus on the overall size they attain, is pertinent in this study, given the use of morphometric characters in

Table 2. Head width of final-instar larvae of *Chlorolestes tessellatus* (Burmeister) for each of spring and summer populations, from high elevation (Hogsback) and low elevation (Oak Valley) localities (*mean* followed by *range* in brackets, all in millimeters).

Site	Season	Degree-hours/day	Head width
Hogsback	Spring (Nov./Dec.)	29.9	4.4 (4.2–4.7)
ditto	Summer (Feb./March)	126.0	4.1 (3.9–4.5)
Oak Valley	Spring (Sept./Oct.)	48.8	4.2 (4.0–4.5)
ditto	Summer (Dec./Jan.)	159.0	4.0 (3.7–4.1)

both the descriptions and key. In as yet unpublished research on the life-cycle of *C. tessellatus* the writer has established that the species is bi-voltine with major adult emergences being in spring and summer. At one of the two Eastern Cape study sites, a high elevation one at 1 180 m.a.s.l. (Hogsback, Amathole Mountains), the emergences are in November/December and February/March respectively. At the second, a low elevation one at 440 m.a.s.l. (Oak Valley, Bloukrans River, near Grahamstown), the emergences are in September/October and December/January respectively. The four sets of measurements provided for *C. tessellatus* (Table 1), are for final-instar larvae collected in these periods.

To determine the influence of water temperature on the size of final-instar larvae, the average daily water temperature (based on continuous recordings using a mercury remote-thermograph and expressed as degree-hours above a 10°C base-line), was calculated for the growth periods of the larvae (from monthly samples) resulting in the spring and summer adult populations at each of the two sites, and compared with head-width measurements (mean and range in millimeters).

Adding to this, final-instar larvae bred through in the laboratory over the period of September–January at approximately 18°C (i.e. average of 192 degree-hours/day) had a head width of 3.7 mm (range: 3.5–3.9 mm; $n=31$) (Table 2).

While the evidence points to water temperature influencing the size of final-instar larvae (i.e. colder water, larger larvae), of more importance in the context of this study is that inter- and intra-site differences in the size of final-instar larvae do occur, and accordingly cognizance must be taken of this in the identification of species.

Finally, need exists for further study, especially of *C. elegans* and *C. tessellatus*. In *C. elegans*, the description is based on a single penultimate-instar larva from Zimbabwe, the northern limit of its geographical range. Specimens from a wider range of sites, including Mpumalanga and Limpopo Province of South Africa, are required. The description of *C. tessellatus* is based on specimens from only two sites in the Eastern Cape Province, and given its wide range clear need exists to include the study of material from at least the Western Cape Province, KwaZulu-Natal and Mpumalanga.

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Appendix. Comparative measurements of six species of *Chlorolestes* Sélys final-instar larvae. For comparative measurements of *C. tessellatus* (Burmeister) vide Table 1.

Measurements	<i>Chlorolestes apricans</i> Wilmot	<i>Chlorolestes conspicuus</i> Sélys	<i>Chlorolestes draconticus</i> Balinsky	<i>Chlorolestes elegans</i> Pinhey	<i>Chlorolestes fasciatus</i> (Burmeister)	<i>Chlorolestes umbratus</i> Sélys
Total length (excl. caudal appendages)	19.3 (16.8–22.0); <i>n</i> =3	29.3 (27.0–31.0); <i>n</i> =19	32.5 (31.0–34.0); <i>n</i> =6	23.5 ¹ ; <i>n</i> =1	25.9 (21.5–28.0); <i>n</i> =27	19.3 (17–22.0); <i>n</i> =13
Head width	3.5 (3.4–3.6); <i>n</i> =3	5.5 (5.0–5.7); <i>n</i> =19	4.5 (4.1–4.7); <i>n</i> =5	4.5; <i>n</i> =1	4.1 (4.0–4.5); <i>n</i> =27	3.5 (3.3–3.7); <i>n</i> =14
Antenna length (total)	4.1 (3.9–4.3); <i>n</i> =3	4.9 (4.3–5.3); <i>n</i> =20	4.5 (4.4–4.6); <i>n</i> =6	no data	4.8 (4.3–5.3); <i>n</i> =26	3.9 (3.6–4.2); <i>n</i> =10
Flagellum length	2.4 (2.3–2.6); <i>n</i> =3	2.8 (2.5–3.1); <i>n</i> =20	2.7 (2.6–2.9); <i>n</i> =6	no data	3.0 (2.6–3.5); <i>n</i> =26	2.3 (2.0–2.5); <i>n</i> =10
Prenotum length	3.1 (3.0–3.2); <i>n</i> =3	4.5 (4.0–4.7); <i>n</i> =20	4.6 (4.5–4.8); <i>n</i> =5	3.8; <i>n</i> =1	3.9 (3.5–4.3); <i>n</i> =26	3.1 (2.9–3.3); <i>n</i> =13
Prenotum width	2.2 (2.1–2.3); <i>n</i> =3	3.6 (3.2–3.7); <i>n</i> =20	3.3 (3.2–3.3); <i>n</i> =5	2.7; <i>n</i> =1	2.7 (2.5–3.1); <i>n</i> =26	2.2 (2.1–2.3); <i>n</i> =13
<i>Wing sheaths length</i>						
Mesothoracic sheaths	4.8 (4.5–5.1); <i>n</i> =3	7.7 (7.1–8.0); <i>n</i> =20	7.0 (6.8–7.0); <i>n</i> =6	6.5; <i>n</i> =1	5.8 (5.3–6.5); <i>n</i> =27	4.7 (4.3–4.9); <i>n</i> =14
Metathoracic sheaths	4.5 (4.3–4.7); <i>n</i> =3	6.9 (6.4–7.4); <i>n</i> =20	6.3 (6.1–6.4); <i>n</i> =6	5.9; <i>n</i> =1	5.3 (4.7–6.0); <i>n</i> =27	4.0 (3.7–4.5); <i>n</i> =14
<i>Caudal appendages</i>						
Median length	3.8 (3.7–3.9); <i>n</i> =3	5.5 (5.0–5.7); <i>n</i> =19	4.7 (4.6–4.7); <i>n</i> =5	4.5; <i>n</i> =1	4.5 (4.1–5.1); <i>n</i> =27	3.4 (3.1–3.9); <i>n</i> =13
Median width	1.3 (1.3–1.4); <i>n</i> =3	2.3 (1.9–2.6); <i>n</i> =19	2.0 (1.8–2.1); <i>n</i> =4	1.8; <i>n</i> =1	1.9 (1.7–2.1); <i>n</i> =27	1.4 (1.1–1.6); <i>n</i> =13
Lateral length	4.1 (4.1–4.2); <i>n</i> =3	5.5 (4.6–5.9); <i>n</i> =19	5.1 (4.9–5.2); <i>n</i> =6	4.8; <i>n</i> =1	5.0 (4.6–5.6); <i>n</i> =26	3.9 (3.4–4.3); <i>n</i> =14
Lateral width	1.3 (1.2–1.4); <i>n</i> =3	2.4 (1.9–2.5); <i>n</i> =19	2.1 (1.9–2.2); <i>n</i> =6	1.8; <i>n</i> =1	1.9 (1.7–2.1); <i>n</i> =26	1.5 (1.4–1.6); <i>n</i> =14

¹Piney (1958) states “Length of full-grown larva, including gills: 27–28 mm, gills about 4.5 mm.”

An annotated checklist of the freshwater bivalves (Mollusca: Bivalvia) of Botswana and Namibia

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An annotated checklist, including 18 species of freshwater bivalve belonging to five families, recorded from Botswana and Namibia, is provided. New morphometric information is provided for the species *Mutela zambesiensis* Mandahl-Barth and *Spathopsis petersi* (von Martens), and features of shell morphology are illustrated for *Pisidium reticulatum* Kuiper using stereoscan microscopy. The majority of species occur in the well-watered northerly regions of these countries. Fifty percent of these are widely distributed tropical African species at, or close to, the southerly limits of their ranges, seven species (39%) are categorised as general 'southern African', and two species (11%) appear to be confined to the south-central African region. Although no endemic bivalve species are recorded from the study area, further research may show that the large *Chambardia* from the Kunene River is *C. moutai* (Darteville) and not *C. wahlbergi* (Krauss) as reported here and that *C. moutai* may be restricted to the Kunene River. Four species are new to Botswana, namely: *Chambardia petersi* (von Martens), *Coelatura mossambicensis* (von Martens), *Pisidium reticulatum* Kuiper and *P. viridarium* Kuiper; and one species to Namibia, namely: *Eupera parasitica* (Deshayes).

Keywords: Mollusca, bivalves, ecology, checklist, Africa, Namibia, Botswana.

INTRODUCTION

Connolly's (1931) report on the non-marine molluscs of Namibia (as South West Africa), and subsequent (1939) monograph dealing with the non-marine molluscs of southern Africa as a whole, have remained the most comprehensive accounts of the freshwater bivalve fauna of Namibia and Botswana (formerly Bechuanaland). This is surprising, in view of the fact that bivalves (Bivalvia) constitute the major component of the benthos of many freshwater habitats, for example, in Lake Kariba, Zimbabwe, where these accounted for 96% of the infaunal biomass (Machena & Kautsky 1988). Much additional material has been collected during the 65 years since Connolly's work. The Unionoida of the northern parts of Botswana and Namibia were included in a review of the superfamily in south-central Africa by Appleton (1979). Further records of these and other families have been given by Appleton *et al.* (2003), Curtis & Appleton (1987), Curtis (1991, 1997, 1999), Daget (1998), de Moor *et al.* (2000), Kuiper (1964, 1966a, 1966b), Mandahl-Barth (1988), and van Bruggen (1980). This checklist updates knowledge of the

freshwater Bivalvia of Botswana and Namibia from these sources and from material collected by staff of the then State Museum of South West Africa (now National Museum of Namibia), the South West African Department of Water Affairs (now Directorate of Water Affairs), the Albany Museum and the AquaRAP 2000 Expedition to the Okavango Delta (Appleton *et al.* 2003).

Namibia is an arid to semi-arid country extending over $11\frac{1}{2}$ degrees of latitude ($17\text{--}28\frac{1}{2}^{\circ}\text{S}$) and, except for the Caprivi Strip, 9 degrees of longitude ($11\text{--}21^{\circ}\text{E}$) (Figure 1). The narrow Caprivi Strip extends $4\frac{1}{2}$ degrees further eastwards to the upper Zambezi River. The freshwaters of Namibia are dominated by four perennial river systems: the Gariep (Orange) River in the south, the Kunene River in the north-west, Okavango and Zambezi Rivers in the north-east, and the Kwando-Linyanti system in the Caprivi. The first mentioned rises in the mountains of Lesotho and the last three mentioned all rise in southern Angola. De Moor *et al.* (2000) provide a useful description of the Kunene River from the Ruacana Falls to the Southern Atlantic.

Botswana (Figure 1) is also arid and covers 9 degrees of latitude ($18\text{--}27^{\circ}\text{S}$) and 9 degrees of longitude ($20\text{--}29^{\circ}\text{E}$). The major source of water is the wetland system in the north-west quadrant of the country, that incorporates the Okavango Delta and the swamps associated with the Linyanti River in the central-north. The catchments of the Kunene, Okavango and Zambezi Rivers drain much of south-central Africa and abut that of the Zaïre River.

The proximity of the rivers in the northern parts of the study area to the Zaïre system (Figure 1), a major centre of mollusc endemism (Brown 1994; Dudley 2001; Pilsbry & Bequaert 1927), is reflected in the high proportion of tropical forms in the bivalve fauna of these systems (i.e. Kunene, Okavango and upper Zambezi Rivers and the wetlands of the Eastern Caprivi) and which is distinct from those in the eastern (Limpopo) and southern (Gariep) systems. In addition to the Okavango Delta in Botswana, there are two other endorreic basins, the ephemeral Cuvelai/Ekuma/Etoshia system in central northern Namibia and the perennial Kwando/Liambezi/Linyanti system in eastern Caprivi. The eastern half of northern Botswana is drained by the eastwards-flowing Limpopo River system. The vast interiors of both countries are drained by numerous seasonal watercourses with many isolated artesian and other springs in the north-central region.

MATERIAL AND METHODS

An annotated checklist to the bivalves of Botswana and Namibia is provided that includes 18 bivalve species in 10 genera and five families. With a few exceptions, genera and species are arranged following Mandahl-Barth (1988); the most comprehensive account of the freshwater bivalves of Africa. It should be noted, however, that the



Figure 1. Map of central and southern Africa, indicating the study area of Botswana and Namibia.

above-mentioned work makes several important changes to the synonymy of the genera *Corbicula* von Mühlfeld, *Eupera* Bourguignat and *Mutela* Scopoli. Locality records cited by Appleton (1979) are not repeated here, except where considered necessary; details of all additional specimens examined during the course of the study are cited below. Illustrations of all species cited here, except *Pisidium reticulatum* Kuiper are provided by Appleton (1996, 2002).

The SEM micrographs of *P. reticulatum* (Figures 6–8), were taken by use of a Philips XL 30 stereoscan microscope at the Centre for Electron Microscopy, Pietermaritzburg Campus, University of KwaZulu-Natal, South Africa.

Abbreviations used in the text: AMGS = Albany Museum, Grahamstown, South Africa; NMNW = National Museum of Namibia, Windhoek, Namibia (formerly the State Museum of South West Africa (SMN)); NMSA = Natal Museum, Pietermaritzburg, South Africa; UKZN = University of KwaZulu-Natal, Durban, South Africa. The prefixes 'KUN' and 'SMN' refer to the accession numbers of specimens housed in the Albany Museum and the National Museum of Namibia, respectively. * = new country record.

SYSTEMATICS

CLASS: BIVALVIA

SUPERFAMILY: UNIONOIDA

FAMILY: UNIONIDAE

Genus: *Unio* Philipsson, 1788

TYPE SPECIES: *Mya pictorum*

Unio caffer Krauss, 1848

DISTRIBUTION: Malawi, Mozambique, Namibia, South Africa, Zambia and Zimbabwe.

MATERIAL: **Namibia:** Gariep (formerly the Orange) River, 1 specimen, between Sandfontein and Grasdrif [SE2817Ad], 1981, J. Coetzee (SMN76090) (NMNW); 4 empty specimens, Lorelei on north bank east of Sendelingsdrif, 28°05'S, 16°53'E, 26.xi.1980, R. van der Westhuizen (UKZN); 7 empty specimens, Vioolsdrift [SE2817Dc], 16.vii.1980, R. Jubb (UKZN).

PUBLISHED RECORDS: Vioolsdrift and Daberas Deposit (28°18'S, 16°49'E) (Palmer 1996).

NOTES: *Unio caffer* is endemic to southern Africa, from approximately 14°S in Malawi, to the Western Cape, South Africa, where it has become rare, or possibly extinct, in some rivers and vleis (J.A. Day pers. comm.). New data support Connolly's (1931, 1939) record from Stolzenfels on the Gariep (Orange) River. In Namibia, therefore, it is found only in the extreme south, in the lower reaches of the Gariep River and its tributaries. The only record from Botswana is as a sub-fossil associated with the southward-flowing Nosob-Hygap River, a tributary of the Gariep River (Connolly 1939). The wide geographical separation of *U. caffer* from the only other species of *Unio* occurring in Africa, i.e. *U. abyssinicus* Martens, 1886, and *U. elongatulus* C. Pfeiffer, 1825, from Ethiopia and north-west Africa (van Damme 1984), led Mandahl-Barth (1988) and Graf & Cummings (2006) to follow Connolly (1925), Modell (1964) in placing it in the genus *Cafferia* Simpson, 1900. They do not refer to a review of the branchial anatomy and systematic position of this species by Heard & Vail (1976), which concluded that it should be retained in *Unio*. This latter opinion is followed here.

Genus: *Coelatura* L. Pfeiffer, 1877

TYPE SPECIES: *Unio aegyptica*

NOTES: The writers follow Rosenberg *et al.* (1990), who pointed out that the commonly used spelling of the name for this large genus, *Caelatura* Conrad, 1853, is incorrect, and that the later name, *Coelatura* L. Pfeiffer, 1877, should rather be used. This genus is widely distributed in Africa, but only two of the many described species are recorded from the study area.

Coelatura kunenensis (Mousson, 1887) (*Unio*)

DISTRIBUTION: Angola, Botswana, Namibia and Zambia.

PUBLISHED RECORDS: **Botswana:** Okavango Delta, sandbanks on the Okavango River, near Shakawe [SE18 21Bd], 8.vi.2000; Moremi Game Reserve, in mud in Gadikwe Lagoon [SE1923Aa] 14.vi.2000 (Appleton *et al.* 2003).

MATERIAL: **Botswana:** Okavango Delta, 4 specimens, Boro River, 19°25'97"S, 22°56'08"E, 13.xii.1996, B.A. Curtis (SMN77019); 2 specimens, same except: 19°27'81"S, 22°57'07"E, 14.xii.1996 (SMN77027); 2 specimens, same except: 19°26'88"S, 22°56'23"E (SMN77031) (all

NMNW); 72 specimens, Chief's Island, Nxaraga Lagoon [SE1923Ca], 10.iii.1984, C.C. Appleton (UKZN); 97 specimens, Thamalakane River at Maun [SE1923Cd], 12–13.iii.1984, C.C. Appleton (UKZN); **Namibia**: Kunene River, 1 pair valves, on banks of floodplain at Palm Grove campsite, Oonjana, 17°00'18"S, 13°25'52"E (site 9 of de Moor *et al.* 2000), 17.xi.1997, F.C. de Moor & S. Bethune (KUN62A) (AMGS). Okavango River, 2 specimens, at: 17°52'67"S, 20°17'64"E, shallow sand, 31.x.1996, B.A. Curtis (SMN76953); 2 specimens, at: 18°00'50"S, 20°44'95"E, shallow with sand, 1.xi.1996, B.A. Curtis (SMN77016); 2 specimens, at: [SE1821Bd], sandbank, 10.xii.1996, B.A. Curtis (SMN76995); 1 juvenile, 45.4 km upstream of Rundu, Mabunya [SE1719Ca], 29.x.1996, B.A. Curtis (SMN76942); 3 specimens, 24.2 km west of Rundu [SE1719Cb], 29.x.1996; B.A. Curtis (SMN76930); 1 juvenile, Rundu slipway [SE1719Dc], 10.vii.1986, P. Skelton & G. Merron (SMN76271); 1 specimen, Ndonga, Omataka confluence [SE 1720Cd], 6.iii.1984, S. Bethune (SMN76122); 16 specimens (including 5 juveniles), Nyangana Omarumba, Okavango floodplain [SE 1820Ba], 12.vi.1983, S. Bethune (SMN76821/SMN76828); 1 specimen, Manuingombe [coordinates unknown], 11.vi.1983, S. Bethune (SMN76822); 17 specimens + 3 left & 1 right valves, Andara Mission [SE1821Ab], 8.iii.1984, C.C. Appleton (SMN76046); 1 specimen, Andara [SE1821Ab], 24.viii.1971, M.J. Penrith (SMN75399); 2 specimens, Popa Falls [SE1821Ba], 21.x.1984, S. Bethune (SMN76109a); 2 specimens, same except: 30.viii.1971, M.J. Penrith (SMN75374); 1 specimen, sandbank below Popa rapids [SE1821Ba], x.1984, P. Skelton & G. Merron (SMN76270) (all NMNW). Eastern Caprivi: 3 specimens, mulapo at Sanzo [SE1721Dc], [undated], A.C. Evans (SMN76823); 1 specimen + 1 left valve, Lizauli [SE1823Ab], 15.vi.1982, T.F. Jackson (SMN76824); 1 specimen, Zambezi floodplain, pool opposite Hippo Island [SE1724Ad], 14.vi.1983, S. Bethune (SMN76825); 1 specimen same except: (SMN76826); 1 juvenile, Zambezi floodplain, off Hippo Island [SE1724Ad], 9.xii.1982, S. Bethune (SMN75948); 6 specimens, including 2 juveniles, Sesheke on Zambezi River [SE1724Ad], [undated], C.J. Schutte (SMN76827); 3 specimens, Lake Lisikeli [SE1724Cb], 14.xii.1982, S. Bethune (SMN76088); 2 juveniles, Kwando River [locality unknown], [undated], C.D. Dettman (SMN76829); 2 specimens, Kwando floodplain, Sitwe [SE1723Cd], 15.xii.1982, S. Bethune (SMN75928); 1 specimen, Zambezi floodplain, Maninge Manzi [SE1724Ad], 10.vi.1983, S. Bethune (SMN76830) (all NMNW).

NOTES: This species was described from the Kunene River, but Mandahl-Barth (1988) followed Connolly (1931, 1939), in uniting it with material from the Okavango and upper Zambezi systems. It appears to be confined to these river systems and is, without doubt, the most common bivalve species in the study area. Both the above and earlier records (Appleton 1979; Appleton *et al.* 2003; Connolly 1931, 1939; Curtis 1997; Curtis & Appleton 1987; van Bruggen 1980) indicate that it occurs at numerous localities on the Kunene, Okavango and upper Zambezi, where these form the northern borders of Namibia and Botswana. These are formed by the Kwando/Linyanti system in eastern Caprivi, the Ekuma floodplain, part of the endorheic Etosha system in Namibia, and the Okavango Delta in Botswana. The species is also common in Iron Age midden sites at Itezithezhi, in the Kafue Valley, Zambia (Appleton 1985).

TAXONOMIC NOTES: As noted by Appleton (1979) and Mandahl-Barth (1988), the shell shape of *C. kunenensis* is variable. Those from the Kunene, Kafue and upper Zambezi Rivers are, in general, shorter and darker than those from the Okavango River and Delta, and thus vary significantly in terms of L/H vs. L ($p < 0.001$) (Appleton 1979). The L/Hmax ratio is higher relative to shell length in the Kunene specimens, particularly in larger examples, than in those from the Okavango River. Nevertheless, Mandahl-Barth (1988) regarded these as the same species, even

though he had not seen material from the Kunene. Young shells, to a length of approximately 20 mm, typically have a chevron sculpture and greenish rays over the shell. As noted above, in terms of morphometrics, however, the populations in the Okavango system appear different from those in the Kunene, Kafue and upper Zambezi systems (Appleton 1979). This requires to be investigated further, as does the relationship between this species and *C. choziensis* (Preston, 1910), from the Luapula River and Lake Bangweulu in northern Zambia (Mandahl-Barth 1968).

Coelatura mossambicensis (von Martens, 1860) (*Unio*)

DISTRIBUTION: Botswana*, Malawi, Mozambique, Tanzania and Zimbabwe.

MATERIAL: **Botswana:** Limpopo River, 1 specimen, Stevensford Game Reserve [2227Db/Dd/2228Ca/Cc], 13.iii.1984, B. van der Waal (UKZN).

NOTES: A south-east African species restricted to the lower Zambezi (including Lake Kariba) in Malawi, Mozambique and Zimbabwe (Appleton 1979; Mandahl-Barth 1988). In the present study area, it is reported only from the Limpopo River in the north-east corner of Botswana. Kenmuir (1980a, 1980b, 1980c), provide information on the ecology, growth and reproductive biology of *C. mossambicensis* in Lake Kariba and Appleton & la Hausse de Lalouviere (1987) on the density of *C. fraumesi* Connolly, 1925, on the Pongolo River floodplain, South Africa.

TAXONOMIC NOTES: Mandahl-Barth (1988) proposed that *C. mossambicensis* be synonymised with the larger *C. fraumesi* which occurs further south in Mozambique, South Africa and Zimbabwe, but until such time as the two species are better known, it seems advisable to treat these as separate species.

FAMILY: IRIDINIDAE

Genus: *Aspatharia* Bourguignat, 1885

TYPE SPECIES: *Margaritana vignonana*

Aspatharia (Aspatharia) pfeifferiana (Bernardi, 1860) (*Margaritana*)

DISTRIBUTION: Widely distributed across central and southern Africa, including: Angola, Botswana, Democratic Republic of Congo, Namibia and Zambia.

MATERIAL: **Botswana:** Okavango Delta, 2 specimens, Thamalakane River, near Maun [SE1923Cd], 12–13.iii.1984, C.C. Appleton (UKZN). **Namibia:** Kunene River, 1 pair valves, on bank of floodplain at Palm Grove campsite, Oonjana, 17°00'18"S, 13°25'52"E (site 9 of de Moor *et al.* 2000), 17.ix.1997, F.C. de Moor (KUN62B) (AMGS). Okavango River, 2 specimens, ±39 km E of Rundu, shallow and sandy, 17°54'61"S, 20°06'43"E, 31.x.1996, B.A. Curtis (SMN76948); 5 specimens, Andara Mission [SE1821Ab], 8.iii.1984, C.C. Appleton (SMN76050) (all NMNW).

NOTES: A distinctive species, widely distributed across southern and central Africa, from Chad to Zimbabwe. In the study area, the above localities, plus those provided by Appleton (1979), Connolly (1931, 1939) and Curtis (1997), indicate that the species occurs in the Kunene, upper Zambezi and Okavango Rivers in Namibia and the Okavango Delta in Botswana. These systems represent the southern range limit of the species in Africa. It is nowhere common and juveniles have not been found. Graf & Cummings (2006) suggest that these may be referable to *A. subreniformis* (Sowerby, 1867) described from Malawi but that more material is needed.

Genus: *Chambardia* Servain, 1890TYPE SPECIES: *Chambardia letourneuxi*

NOTES: The use of the generic name *Chambardia* is contentious and requires justification. Daget (1998) revived the name *Chambardia* Servain (1890) for the following two species despite its earlier rejection by van Damme (1984), Mandahl-Barth (1988) and Appleton (1996) in favour of *Spathopsis* Simpson, 1900. Daget (1998) argued that because the types of both genera were generally considered subspecies of *S. wahlbergi* (Krauss, 1848), they were synonymous and that the older synonym, *Chambardia*, should have priority. Mandahl-Barth (1988) did not mention *Chambardia* at all, recognising the genus *Spathopsis* and two species-groups within it, the Wahlbergi- and Rubens-groups. These are included below under the name *Chambardia*, but only the former group is found in southern Africa and the two species allocated to it both occur in the study area. Appleton (2002) followed Daget's 1998 use of the name *Chambardia* instead of *Spathopsis* and the writers also do so here.

Chambardia wahlbergi (Krauss, 1848) (*Iridina*)

DISTRIBUTION: Widely distributed across Africa, including: Angola, Botswana, Chad, Egypt, Kenya, Malawi, Mozambique, Namibia, Senegal, South Africa, Tanzania and Zimbabwe.

NOTES: This is the largest freshwater bivalve in Africa. This widely distributed species was, as reported by Appleton (1979), formerly known as *Aspatharia* (*Spathopsis*) *wahlbergi* or *Spathopsis wahlbergi*, and is apparently uncommon in the study area. It was collected from the Kunene River at Ruacana (SMN75597, 17°24'05"S, 14°12'55"E) and from the upper Kunene River in southern Angola by Darteville (1939). There is a single record from the Kavango River at its junction with the Omataka-Omarumba (Ndonga, 17°57'S, 20°59'E) (Connolly 1939), but it has not been reported again from this river and has never been collected in the Okavango Delta. Appleton (1979) recorded it from the Nata River in north-eastern Botswana; the westernmost tributary of the eastwards-flowing Limpopo system. Both Mandahl-Barth (1988) and Daget (1998) recognised six extant geographical subspecies of this species, two of which occur in the study area. The southernmost subspecies, *C. wahlbergi wahlbergi* (Krauss, 1848), occurs from South Africa to southern Tanzania and the second, *C. wahlbergi welwitschi* (Morelet, 1868), in Angola and the Kunene River, but is of doubtful validity (*vide* Mandahl-Barth 1988: 68, fig. 26). Although Appleton (1979) referred to material from the Kunene River as *A. wahlbergi*, he drew attention to the fact that these specimens had a lower L/H ratio (1.75–1.86) than those from other systems to the east (mean for 10 adult specimens from Nseleni River, KwaZulu-Natal, South Africa = 2.05 ± 0.04 , $n=10$) and thus resembled *C. montai* recorded from the upper Kunene by Darteville (1939). Graf & Cummings (2006) identified the Kunene material examined by them as *C. montai* (Darteville, 1939), but did not record it beyond this system. The absence of this high-shelled *Chambardia* from the upper Zambezi is surprising bearing in mind past, and perhaps present, connections between the upper tributaries of the two (Dudley 2001; Skelton *et al.* 1985). The relationship between *C. wahlbergi* and *C. montai* in south-central Africa needs critical examination.

Chambardia petersi (von Martens, 1859) (*Spatha*)

DISTRIBUTION: South Africa, Botswana*, Malawi, Mozambique, Tanzania and Zimbabwe.

MATERIAL: **Botswana:** Limpopo River, 3 specimens, Stevensford Game Reserve [coordinates unknown], 13.iii.1984, B. van der Waal (UKZN).

NOTES: Formerly referred to as *Aspatharia* (*Spathopsis*) *petersi*, this is a smaller and narrower species than the above, with the dorsal and ventral margins virtually parallel. As far as is known,

C. petersi is restricted to the catchments of the lower Zambezi, Limpopo and Incomati Rivers in Malawi, Zimbabwe, Mozambique and South Africa. The only record from the study area comprises three specimens from the Limpopo River system in north-eastern Botswana. As *C. petersi* is infrequently found, the dimensions of these three specimens are provided here: 68.9 x 31.1 x 19.2 mm, L/H ratio 2.22, umbo at 0.36 length; 64.8 x 27.5 x 16.4 mm, L/H ratio 2.36, umbo at 0.35 length; 62.7 x 27.6 x 16.5 mm, L/H ratio 2.27, umbo at 0.31 length ($n=3$). These measurements agree with those provided for eight specimens of *C. petersi* from the Zambezi River at Tete, Mozambique, by von Martens (1897) and for a large collection from an Iron Age archaeological site on the banks of the Shingwedzi River, Limpopo Province, South Africa (C.C. Appleton & I. Plug unpubl.) (*vide* Figure 2 below). The L/H ratio of these last mentioned shells decreased as the animal grew, from 2.4–2.6 mm at a valve length of 54–65 mm to 1.95–2.2 mm at a length of 105–125 mm. Over this size range, therefore, the shell becomes narrower as it grows and following the limited data given by von Martens (1897), the umbones move slightly closer to the middle of the valves as valve length increases. The Botswana specimens' valve lengths of 60–70 mm lie in the upper half of the species' size range. As *C. petersi* is a poorly characterised species, the writers include measurements of the material from the Shingwedzi River, South Africa, referred to above. Figure 2 illustrates valve length plotted against maximum height and Figure 3 L/H plotted against length ($n=65$ in both cases).

Genus: *Mutela* Scopoli, 1777

TYPE SPECIES: *Mytilus dubius*

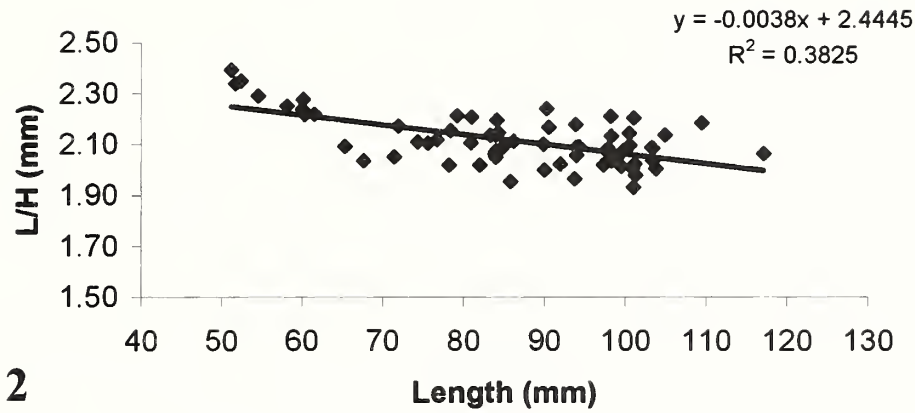
Mutela zambesiensis Mandahl-Barth, 1988

DISTRIBUTION: Angola, Botswana, Namibia, Zambia and Zimbabwe.

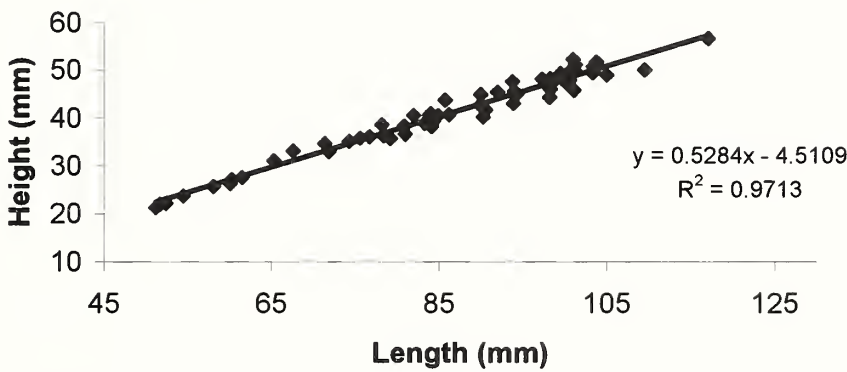
PUBLISHED RECORDS: **Botswana:** Guma Lagoon (lower panhandle) [SE1822Cd], 12.vi.2000; Moremi Game Reserve, in mud in Gadikwe lagoon [SE1923Aa], 14.vi.2000 (Appleton *et al.* 2003).

MATERIAL: **Botswana:** Okavango Delta, 7 specimens, Thamalakane River bridge, near Maun [SE1923Cd], 12–13.iii.1984, C.C. Appleton (UKZN); 10 specimens, Chief's Island, Nxaraga lagoon [SE1923Ca], 14.iii.1984, C.C. Appleton (UKZN); 1 specimen, Khumaga, Boteti River, in sand and peaty detritus [SE2024Ad], 24.xii.1980, P.E. Reavell (UKZN); 1 specimen, Santantadibe River, 19°34'76"S, 23°22'50"E, 14.xii.1996, E. Taylor (SMN77024) (NMNW); 9 specimens, Gadikwe lagoon [SE1923Aa], vi.2000, C.C. Appleton (UKZN). **Namibia:** Kunene River, 2 specimens, hippo pools below Ruacana Falls [SE1714Ac], 4.x.1987, B.A. Curtis (SMN76508); Namibia: Okavango River, 1 specimen, Shigaya [SE1720dC], 2.xi.1996, B.A. Curtis (SMN76977) (all NMNW). Eastern Caprivi, 3 specimens, Singalamwe [SE1723Cb], [undated], A.C. Evans (SMN76831); 2 specimens, Singalamwe Mulapo [SE1723Cb], Kwando floodplain, 22.x.1987, B.A. Curtis (SMN76564); 2 specimens, Lizauli near Kwando River [SE1823Ab], 15.vi.1982, T.F. Jackson (SMN76832); 1 specimen, Sesheke on Zambezi River [SE1724Ad], [undated], C.J. Schutte (SMN76833); 1 specimen, Zambezi River opposite Lisikili [SE1724Cb], 8.xi.1986, C.H. Schlettwein, N. Lemmer & J. Coetzee (SMN76324) (all NMNW).

TAXONOMIC NOTES: This species is characterised by the very low umbone. As the shell grows, the maximum height (Hmax) moves closer to the posterior end of the shell which gives old shells a distinctly rugose and truncate appearance posteriorly (Figure 4). In this respect they resemble *M. dubia*, as illustrated by Appleton (1979), Daget (1964), and Pilsbry & Bequaert (1927, plate 38). In the series of 90 individuals available from the Okavango Delta and



2



3

Figure 2–3. *Chambardia petersi* (von Martens), from the Shingwedzi River, Limpopo Province, South Africa (C.C. Appleton & I. Plug unpubl.). 2, L/H plotted against L ($Y = 0.5284x - 4.5109$; $R^2 = 0.9713$); 3, H plotted against L ($Y = -0.0038X + 2.4445$; $R^2 = 0.3825$)

adjacent eastern Caprivi wetlands, all shells less than 85–90 mm in length resemble *M. rostrata*, while many, but not all of the longer shells resemble *M. dubia*. Blay (1989) and Daget (1964) demonstrate little variation in the shape of the shells of two West African mutelids, *Mutela rostrata* and *Aspatharia sinuata* from geographically separate populations in ecologically different habitats. They argue that this limited between-habitat variability in shell dimensions indicated that the environmental effect is small, resulting in stable shapes that should be considered characteristic for the species. Indeed, Blay (1989) calculated a coefficient of variation of <10% in the mean length:height ratios of shells of both sexes from five widely separate populations of *A. sinuata*. Thus, the differences between the regressions calculated by Daget (1964) for West African species *M. dubia* and *M. rostrata* are taken to reflect characteristic differences in shell length/height relationships. Although he used power curves to describe these relationships, they are very close to straight lines, especially for *M. rostrata*. His equations, solved for shell length (L), are given together below, with L/height (H) and length/width (W) ratios: *M. dubia*: $L = 3.715 H^{0.893}$; L/H ratio 2.77–3.32; L/W ratio

4.67–6.41. *M. rostrata* (two geographically separate populations combined): $L = 3.145 H^{0.99}$; L/H ratio 2.65–3.17; L/W ratio 4.63–6.37. The writers therefore follow the above authors in presenting comparable morphometric data for the series of *M. zambesiensis* shells from the Okavango River and Delta, and Linyanti swamps of eastern Caprivi, in an attempt to further characterise this species which appears to be confined to the study area. The best fit linear regression between *M. zambesiensis* shell length (L) and maximum height (Hmax) is given by $L = H_{\max} + 0.8191/0.3966$ ($L = 0.3966H_{\max} - 0.8191$) (Figure 5) with a correlation coefficient $R^2 = 0.9349$ ($n=90$). The L/H ratio varied from 2.26 to 3.11, a range which is similar to both *M. rostrata* and *M. dubia*, but the L/W ratio varied between 3.80 and 7.48, which is a broader range than either of these species. The umbones fall between 0.19 and 0.30 ($mean=0.25$) of the length from the anterior end. They were almost always eroded, especially in larger shells, so that their exact position could often only be determined internally. The angles formed by the dorsal/anterior and dorsal/posterior margins were distinct only on shells <85 mm in length, and not in longer ones. The observation by Mandahl-Barth (1988) that as shell size increases, the dorsal margin becomes more sloping, so that Hmax moves closer to the posterior end was confirmed, but only for small and medium-sized shells. Plotting the position of Hmax (expressed as a percentage of total shell length from the posterior end) against shell length (Figure 4) showed that Hmax did move posteriorly, but only in shells up to about 80 mm. When longer shells were included, the relationship could be described by a 2nd order polynomial equation: $H_{\max} = 0.0029x^2 - 0.4143x + 39.551$ though with a low correlation, $R^2 = 0.2576$ ($n=18$). For shells longer than ± 80 mm, Hmax appears to move anteriorly again, but to differing extents in different individuals. In the two specimens available from the Kunene River (SMN76508), Hmax lay at 0.18 and 0.22 from the posterior end respectively; closer to the posterior end than any from the Okavango system.

NOTES: Mandahl-Barth (1988) ‘reluctantly’ described *M. zambesiensis* as a new species from the Zambezi River, “... between Kariba and Chirundu ...”, i.e. downstream of Lake Kariba, Zimbabwe; and from Singalangwe (=Singalamwe), close to the Kwando River in eastern Caprivi, Namibia. It is, in fact, the only species of *Mutela* he recognised from southern Africa. The principal justification for designating the new species was that the southern African shells had features in common with two widespread tropical African species, *M. dubia* (Gmelin, 1791), and *M. rostrata*, but conformed precisely to neither. Younger valves resembled members of Mandahl-Barth’s (1988) Rostrata-group of *Mutela* (which includes *M. mabilli*, reported from the study area by Connolly 1931, 1939), whereas older valves were closer to *M. dubia*, which was reported from the study area by Appleton (1979). Curtis (1991) thus recorded both *M. dubia* and *M. rostrata* from the Namibian section of the Kavango River. *Mutela zambesiensis* is known from the Kunene, Okavango (though not commonly from the stretch forming the Namibia/Angola border), and upper Zambezi Rivers, as well as the Chobe/Linyanti system of Eastern Caprivi (Appleton 1979; Appleton *et al.* 2003; Connolly 1931, 1939; Curtis & Appleton 1987; van Bruggen 1980). *Mutela zambesiensis* thus has a south-central African distribution, rather similar to another unionoidan bivalve, *Coelatura kunenensis*. This may be associated with specificity in respect of their fish hosts during their parasitic larval phase, as well as to river capture and changes in river courses in the region in the past. A few specimens of *Mutela* collected in the lowveld of Mpumalanga Province, South Africa, may also belong to *zambesiensis* (*vide* Discussion). Van Damme’s (1984) statement that *Mutela* reaches its southern limit in Lake Malawi and the Shire River is clearly incorrect.

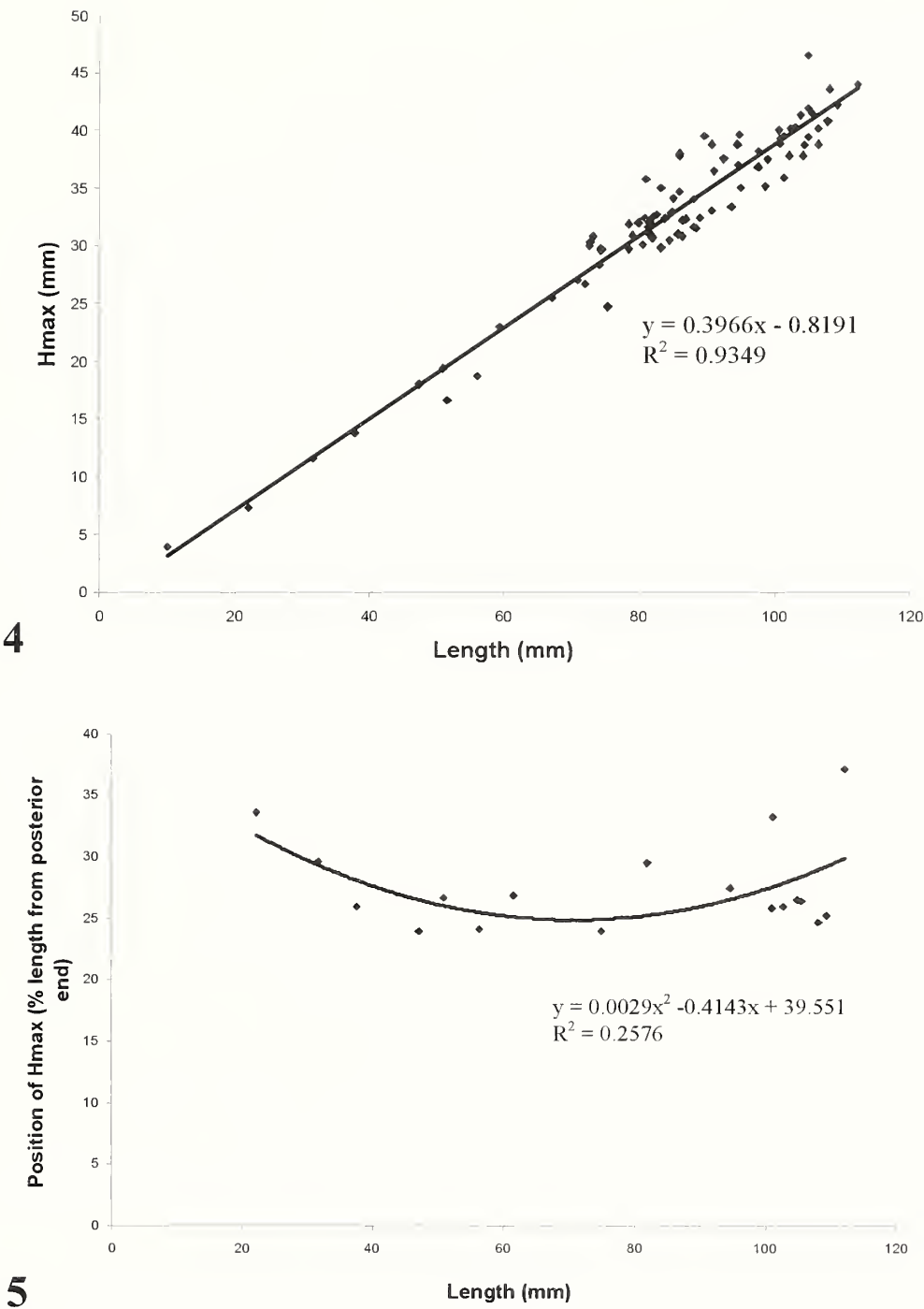


Figure 4–5. *Mutela zambesiensis* Mandahl-Barth. 4, Hmax plotted against L. ($Y = 0.3966x - 0.8191$; $R^2 = 0.9349$); 5, position of Hmax on dorsal margin (% length from posterior end) plotted against L. ($Y = 0.0029x^2 - 0.4143x + 39.551$ ($R^2 = 0.2576$)).

FAMILY: ETHERIIDAE

Genus: *Etheria* Lamarck, 1807TYPE SPECIES: *Etheria elliptica**Etheria elliptica* Lamarck, 1807

DISTRIBUTION: Widely distributed in sub-Saharan Africa, including: Angola, Democratic Republic of Congo, Egypt, Ethiopia, Madagascar, Namibia, Nigeria, Senegal, Tanzania, Uganda and Zambia.

MATERIAL: **Namibia:** 1 upper valve, beach at waterfalls below Sera Cafema, 17°09'43"S, 12°08'57"E, 14.xi.2000, K. Schachtschneider (KUN186A) (AMGS). Kunene River, 4 upper valves, immediately below Ruacana Falls [SE1714Ac], 16.xii.1986, B. van der Waal (SMN76834) (NMNW); 3 complete specimens, Croc pool below Ruacana Falls, 17°24'05"S, 14°12'55"E, 11.xi.1997, F.C. de Moor & S. Bethune (KUN6A); 7 upper valves, along banks of floodplain at: 17°02'00"S, 13°28'53"E (site 22 of de Moor *et al.* 2000), 27.xi.1998, F.C. de Moor & S. Bethune (KUN137) (all AMGS).NOTES: An unmistakable species, characterised by irregular valves that frequently assumed their shape from the substratum. The lower valve, which may be either the left or right, is cemented to the substratum, usually rock or older shells. The attached valve is the larger and thicker of the two and often exhibits a distinctive lamellate structure, but in the three KUN6A specimens it is flat. The umbo and hinge plate of the upper valve usually protrude over the lower one. The largest of the KUN6A specimens measured 92.1 x 51.5 x 23.0 mm ($n=1$). Known by the vernacular name 'African river oyster', *E. elliptica* is widely distributed over tropical Africa and Madagascar. In the study area it occurs only in the rapids of the lower Kunene River, i.e. below Ruacana Falls at an altitude of approximately 780 m.a.s.l., as previously reported by Appleton (1979), de Moor *et al.* (2000) and Haas (1936). Curtis (1999) reported large specimens attached to the Calueque-Olushandja Canal, which transfers water from the Kunene River to the Olushandja Dam in north-western Namibia. The Kunene River is the southernmost locality for *E. elliptica*, but the population is threatened by the proposed construction of a second hydroelectric scheme on the Kunene River (*vide* de Moor *et al.* 2000).

SUPERFAMILY: CORBICULOIDEA

FAMILY: CORBICULIDAE

Genus: *Corbicula* von Mühlfeld, 1811TYPE SPECIES: *Corbicula fluminalis**Corbicula fluminalis africana* (Krauss, 1848) (Cyrena)

DISTRIBUTION: Widely distributed in sub-Saharan Africa, including: Botswana, Malawi, Mozambique, Namibia, South Africa and Zimbabwe.

PUBLISHED RECORDS: **Botswana:** Shakawe [SE1821Bd], in sand in the Okavango Delta panhandle, 08.vi.2000 and Moremi Game Reserve [SE1923Ab], Maunachira Channel, 14.vi.2000 (Appleton *et al.* 2003).MATERIAL: **Botswana:** Okavango Delta, 13 specimens + 3 right valves, Thamalakane River near Maun [SE1923Cd], 12–13.iii.1984, C.C. Appleton (UKZN). **Namibia:** Gariep (Orange) River, 1 specimen + 1 worn left valve, Vioolsdrift [S2817Dc], 16.vii.1980, R. Jubb (UKZN). Kunene River: 2 juveniles, Stein Guard Post, hand-collected off stones in slow current, 17°25'55"S,

13°59'05"E, 12.xi.1997, F.C. de Moor (KUN18G); 1 juvenile, stones-in-current, 17°11'07"S, 13°35'52"E, 16.xi.1997, F.C. de Moor & S. Bethune (KUN48R); 3 juveniles, amongst submerged vegetation (*Hydrostachys polymorpha*) on stones at Otjihandjaveru rapids, 17°05'58"S, 13°31'11"E, [undated], F.C. de Moor & S. Bethune (KUN51R); 2 juveniles, at: 17°00'18"S, 13°25'52"E, sediments of pool on floodplain (at site 9 of de Moor *et al.* 2000), 17.xi.1997, F.C. de Moor & S. Bethune (KUN61B) (all AMGS). Okavango River: 1 specimen, shallow water, 24.2 km west of Rundu [SE1719Dc], 29.x.1996, B.A. Curtis (SMN76932); 1 specimen, Kapaku [SE1719Cb], 10.vi.1983, S. Bethune (SMN76836); 1 juvenile, shallow water at: 17°58'63"S, 20°38'32"E, 1.xi.1996, B.A. Curtis (SMN76972) (all NMNW). Eastern Caprivi: 3 specimens, Zambezi floodplain, pool opposite Hippo Island [SE1724Ad], 14.vi.1983, S. Bethune (SMN76835); 1 specimen, Zambezi River, Kalambeza Island [SE1724Da], 5.xi.1986, B.A. Curtis (SMN76280); 3 specimens, Kwando River [locality unknown], [undated], A.C. Evans (SMN76837) (all NMNW).

TAXONOMIC NOTES: Mandahl-Barth (1988) followed Haas (1936) in dividing the many described species of *Corbicula* from Africa into two species-groups: the Fluminalis-group, based on the Asian *C. fluminalis*, and the Astartina-group, restricted to Africa. Three subspecies are recognised in the Fluminalis-group, with the southern African species previously known as *C. africana*, included in *C. fluminalis africana*. The remaining two subspecies occur in East and central African lakes. *Corbicula f. africana* is distributed from the Shaba Province of the Democratic Republic of Congo to South Africa. The remaining species of *Corbicula* known from Africa, *C. astartina*, has not been reported from the study area, although Mandahl-Barth (1968) reported it (as *C. rosini*) from Lake Bangweulu in northern Zambia. *Corbicula fluminalis* should not be confused with another Asian species, the similarly-named *C. fluminea* (Müller, 1774). As far as is known, *C. fluminea* has not been found in Africa, although it has become invasive, reaching pest status elsewhere. The Okavango specimens are relatively small, the largest available measuring 15.0 x 12.2 x 7.9 mm ($n=14$), and have a distinctly triangular shell. Sculpture is well developed and all shells are olive green/yellow externally, with the internal shell between the pallial line and the umbone pale mauve.

NOTES: In southern Africa, *C. fluminalis* is both widespread and variable and in the study area occurs in all major river systems. It also occurs in the Gariep (Orange) River (Palmer 1996), but there is only one record from the Namibian section. Curtis (1999) reported that *C. fluminalis* had spread from the Kunene River to the Calueque-Olushandja Canal.

FAMILY: SPHAERIIDAE

Genus: *Sphaerium* Scopoli, 1777

TYPE SPECIES: *Tellina cornea*

NOTES: Since both *Sphaerium capense* and *S. incomitatum* often occur sympatrically in the same habitats, detailed descriptions of the shells of these species were provided by Appleton (1996, 2002). Both species have been collected in the Okavango system, but neither has been found in the Kunene River.

Sphaerium capense (Krauss, 1848) (*Cyclas*)

DISTRIBUTION: Botswana, Madagascar, Namibia, South Africa, Zambia and Zimbabwe.

PUBLISHED RECORDS: **Botswana:** Guma Lagoon, in sediment-filled crevices between culms of *Cyperus papyrus*, exposed sandy shoreline and permanent small lagoon, between Guma and

Nqoga Channel [SE1822Cd], 11–12.vi.2000; Gadikwe Lagoon [SE1923Aa], 14.vi.2000 (Appleton *et al.* 2003).

MATERIAL: **Botswana:** Okavango Delta, 1 specimen, Boro River [SE1922Bd], 15.xii.1996, B.A. Curtis (SMN77035); 2 specimens, rainfilled backwater at: 19°37'94"S, 20°24'44"E, 13.xii.1996, E. Taylor (SMN77001) (all NMNW). **Namibia:** Kavango River, 5 specimens, small muddy pool, backwater at Cuito confluence below malaria camp at Katere [SE1820Bb], 3.xi.1996, B.A. Curtis (SMN76983) (all NMNW). Eastern Caprivi: 3 specimens, Kwando River floodplain, [locality unknown], [undated], C.D. Dettman (SMN76838); 4 specimens, pools in Kwando floodplain near Sietwa Camp, [SE1823Ab], 18.x.1987, B.A. Curtis & A.C. Evans (SMN76527a) (all NMNW).

NOTES: Shells generally cream/white in colour, but some are dull brown. Widely distributed over southern Africa, from Zambia to South Africa and Madagascar; often occurring in large numbers and sometimes together with the following species, *S. incomitatum*. Connolly (1931) recorded *S. capense* from two localities in Namibia, Grootfontein in the north-east and Seeheim in the south, both far from the present records. The type locality is the Knysna River on the southern coastal strip of South Africa, where the species was noted by Krauss to be common (*vide* Herbert & Warén 1999, as *Cyclas capensis*). The type locality may, however, be erroneous, as it has not been reported from the area since and although Krauss undoubtedly collected freshwater molluscs in the Knysna River (*vide* Herbert & Warén 1999), he also collected extensively in the environs of Durban, a more acceptable locality (*vide* entry for *Eupera ferruginea*).

Sphaerium incomitatum (Kuiper, 1966a) (*Pisidium*)

DISTRIBUTION: Botswana, Democratic Republic of Congo, Namibia, South Africa, Zambia and Zimbabwe.

PUBLISHED RECORDS: **Botswana:** Guma Lagoon (sandy shoreline) and mud in small lagoon between Guma and Nqoga Channel [SE1822Cd], 12.vi.2000; Gadikwe Lagoon [SE1923Aa], 14.vi.2000 (Appleton *et al.* 2003).

MATERIAL: **Botswana:** Okavango Delta, 3 specimens, Boro River [SE1922Bd], 15.xii.1996, B.A. Curtis (SMN77035) (all NMNW). **Namibia:** Okavango River, 1 specimen, south bank, sandy substratum at: 17°56'96"S, 21°04'99"E, 3.xi.1996, B.A. Curtis (SMN76979) (NMNW). Eastern Caprivi: 1 specimen, Kwando floodplain [locality unknown], [undated], C.D. Dettman (SMN76839); 6 specimens, pools in Kwando floodplain near Sietwa Camp [SE1823Ab], 18.x.1987, B.A. Curtis & A.C. Evans (SMN76527b) (all NMNW).

NOTES: As with the preceding species, *S. incomitatum* is distributed over southern and south-central Africa, from South Africa to northern Zambia and Shaba Province of the Democratic Republic of Congo.

Genus: *Pisidium* C. Pfeiffer, 1821

TYPE SPECIES: *Tellina amnica*

Pisidium ovampicum Ancey, 1890 (*Pisidium*)

DISTRIBUTION: Ethiopia, Kenya, Madagascar, Namibia, South Africa and Uganda.

NOTES: The type locality of this species, Omambonde [Okambonde 1716Cc or Omubonde 1714Ad] in Ovambo, Namibia (Connolly 1931, 1939; Kuiper 1964, 1966a), remains the only record for the study area. It is, however, 'vague' (Connolly 1931) and cannot be precisely

located, although it is possibly a Herero name. Connolly (1931) commented, as did Mandahl-Barth (1988), that this species with its rounded shape and almost centrally-placed umbones closely resembled small examples of the genus *Sphaerium*. Mandahl-Barth (1988) listed the “... poor size and, as a rule, the white shell ...” as characters of *P. ovampicum* that distinguish it from juvenile *Sphaerium* of the same size, although it is not clear what he exactly meant by ‘poor size’. The species is distributed from South Africa to Ethiopia and Madagascar.

Pisidium casertanum (Poli, 1791) (*Cardium*)

DISTRIBUTION: Widely distributed across Africa, including: Canary Is., Ethiopia, Kenya, Madagascar, Madeira Is., Namibia, Rwanda, South Africa, Sudan, Tanzania, Uganda and Zimbabwe.

NOTES: A species described from Europe, but widely distributed in Africa from South Africa to Ethiopia and north-west Africa. The only locality in the study area is a single record from Grootfontein, Namibia (Kuiper 1964, 1966a). Mandahl-Barth (1988) noted that this is the most enigmatic of the African *Pisidium* spp., as it lacks any clear distinguishing features.

Pisidium langleyanum Melvill & Ponsonby, 1891 (*Pisidium*)

DISTRIBUTION: Lesotho, Namibia, South Africa and Zambia.

MATERIAL: **Namibia**: 4 specimens, marshy area below dam on farm Strydfontein [SE1918Ca], 3.ix.1988, B.A. Curtis (SMN76625); 2 specimens, spring on farm Spitzkop [SE1918Ac], 5.ix.1988, B.A. Curtis (SMN76639) (all NMNW).

NOTES: In the study area this species is only known from Namibia, and only from isolated waterbodies on two farms in the Grootfontein District. It has not been collected from any natural watercourses. There is no thickening (=‘nodule’ of Mandahl-Barth 1988), at the anterior end of the posterior lateral tooth (p3) in the right valve. The presence of such a nodule is diagnostic for the similar species, *P. viridarium* (*vide infra*). *Pisidium langleyanum* is restricted to southern Africa, from South Africa to northern Zambia.

Pisidium viridarium Kuiper, 1956 (*Pisidium*)

DISTRIBUTION: Widely distributed across southern and central Africa, including: Botswana*, Democratic Republic of Congo, Ethiopia, Kenya, Lesotho, Madagascar, Rwanda, South Africa, Uganda and Zimbabwe.

PUBLISHED RECORDS: **Botswana**: Okavango Delta, Moremi Game Reserve Reserve [SE1923Ab], in sediments of slowly-flowing Maunachira Channel, 14.vi.2000 (as *Pisidium* sp., Appleton *et al.* 2003).

MATERIAL: **Botswana**: Okavango Delta, 5 valves, Nxaraga Lagoon, Chief’s Island [SE1923Ca], in mud amongst vegetation in shallow water, iii 1984, C.C. Appleton (UKZN).

NOTES: Conspicuous ferruginous deposits are present on the posterior and dorsal parts of the shells, corresponding to those aspects that protrude from the substratum when the live animal is partially buried. Recent collecting (H. Dallas pers. comm. 2004), has shown *P. viridarium* to occur more widely in the Moremi area of the Delta than the above records indicate. It is distributed from South Africa to Kenya.

TAXONOMIC NOTES: Mandahl-Barth (1988) followed Kuiper (1964, 1966a), in noting that *P. viridarium* is closely allied to the central African species *P. kenianum*, but may be separated from the latter on the basis of a small nodule in front of the posterior lateral tooth (p3) in the right valve. Mandahl-Barth (1988) went further and proposed that *P. kenianum* is a northerly race of the southern African *P. langleyanum*. Until these questions have been clarified, the writers retain the name *viridarium* for the most common *Pisidium* in the Okavango Delta.

Pisidium (*Parapisidium*) *reticulatum* Kuiper, 1966b

DISTRIBUTION: Botswana*, Madagascar, Malawi and Zimbabwe.

PUBLISHED RECORDS: **Botswana**: Okavango Delta, Moremi Game Reserve [SE1923Ab], from sediments at the margin of the Maunachira Channel, 14.vi.2000, [C. Appleton & B. Curtis] (Appleton *et al.* 2003).

NOTES: A little known, but unmistakable species, described from material collected in the Gwebi River, Zimbabwe, and from Nossi-Bé Island [=Nosy Be], Madagascar. Mandahl-Barth (1988) cites an additional record from the southern part of Lake Malawi. The single specimen from Botswana (cited above) was collected together with *Corbicula fluminalis*, *Eupera parasitica* and *P. viridarium* (Appleton *et al.* 2003).

TAXONOMIC NOTES: Recognised by its external ligament and unique reticulate sculpture. The only other southern African *Pisidium* with an external ligament is the widespread species *P. pirothi*. Figures 6–8 illustrate three aspects of paratype No. 4 of *P. reticulatum* collected in Nossi-Bé Island, Madagascar, by F. Stormühlner in 1958, housed in NMSA (L5669/T1799).

Genus: *Eupera* Bourguignat, 1854

TYPE SPECIES: *Pisidium moquinianum*

NOTES: On the basis of their original descriptions, the two species of *Eupera* reported from southern Africa, namely: *E. ferruginea* and *E. parasitica*, are separable on shell shape and sculpture. Mandahl-Barth (1988) did not recognise *E. parasitica*, however, and included this as a synonym of *E. ferruginea*. Both species names are applied here, but it is noted that a revision of the African species of the genus is required (*vide infra*).

Eupera ferruginea (Krauss, 1848) (*Cyclas*)

DISTRIBUTION: Widely distributed across Africa, including: Botswana, Egypt, Ethiopia, Madagascar, Mauritius Is., Mozambique, Namibia and South Africa.

PUBLISHED RECORDS: **Botswana**: Okavango River, upper panhandle [SE1821Bd], 7–8.vi.2000 [C. Appleton & B. Curtis] (Appleton *et al.* 2003).

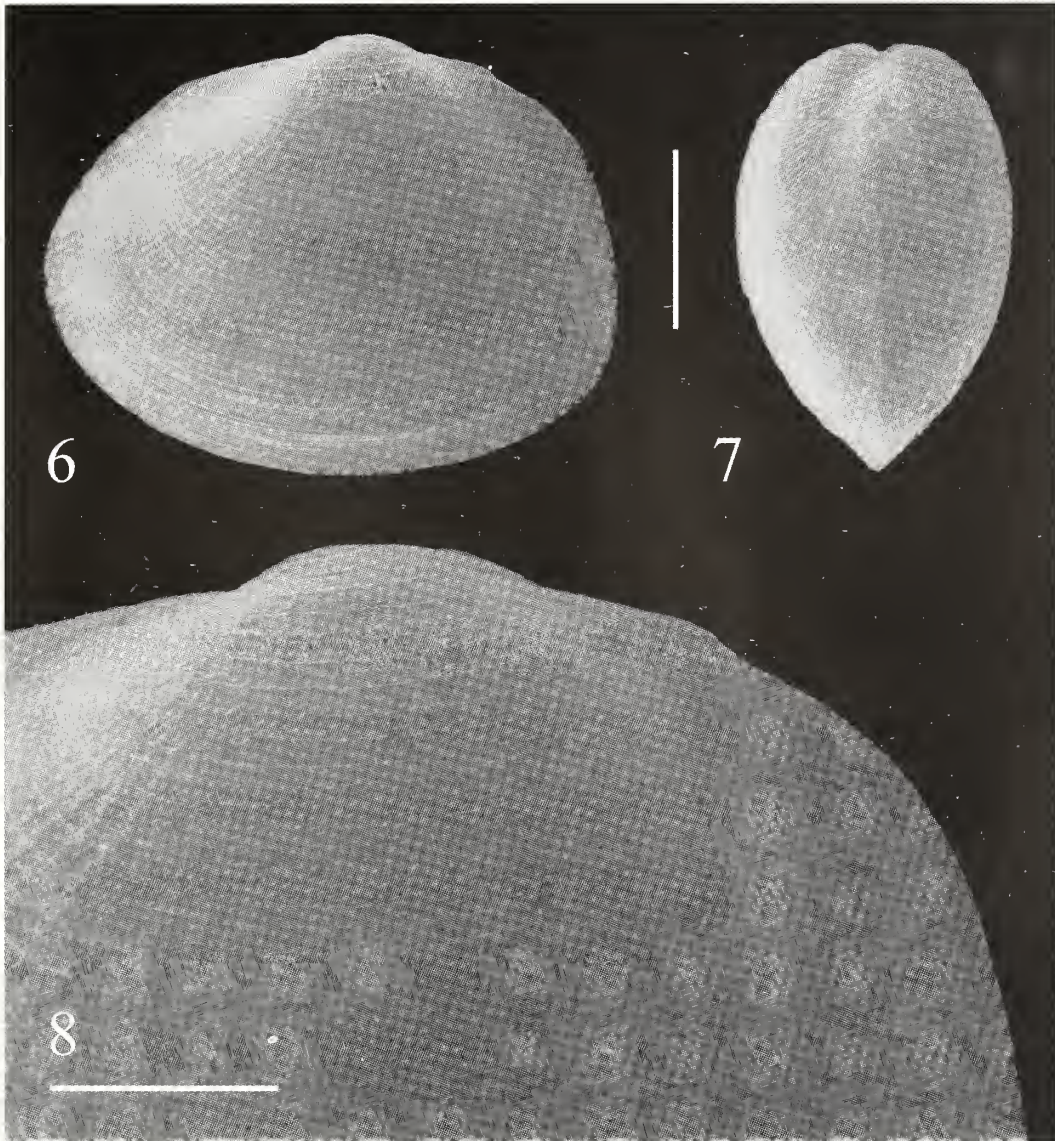
MATERIAL: **Botswana**: Okavango Delta, 1 empty specimen, Okavango Delta panhandle at Shakawe [SE1821Bd], 10.xii.1996, B.A. Curtis (SMN76994) (NMNW). **Namibia**: Okavango River, 1 specimen, Popa Falls [SE1821Ba], 21.x.1984, S. Bethune (SMN76108b); 1 specimen, same except: 14.xi.1983 (SMN76412) (both NMNW). Eastern Caprivi: 7 specimens, pools in Kwando floodplain near Sietwa Camp [SE1823Ab], 18.x.1987, B.A. Curtis & A.C. Evans (SMN76524) (all NMNW).

NOTES: *Eupera ferruginea* has a pan-African distribution, from South Africa to Egypt, but in the study area has only been collected in the Okavango system and the Eastern Caprivi wetlands. It is found in a variety of habitat types: out-of-current stream sediments, between rocks in rapids, such as Popa Falls on the Okavango River and silt-filled crevices between *Cyperus papyrus* culms. As in *Sphaerium capense*, the type locality of this species is the Knysna River, South Africa, but it has not been collected since in that area and may be an error (*vide* Herbert & Warén 1999, as *Cyclas ferruginea*). The discussion under *S. capense* also applies to this species.

Eupera parasitica (Deshayes, 1854) (*Pisum*)

DISTRIBUTION: Botswana, Egypt, Namibia* and Uganda.

PUBLISHED RECORDS: **Botswana**: Moremi Game Reserve [SE1923Ab], from sediments at the margin of the Maunachira Channel, 14.vi.2000, [C. Appleton & B. Curtis] (Appleton *et al.* 2003).



Figures 6–8. SEM micrograph of *Pisidium reticulatum* Kuiper (paratype No. 4, NMSA). 6, left valve; 7, posterior aspect, indicating moderate inflation of closed valves; 8, detail of sculpture and external ligament. Scale bars: 6 & 7 = 1 mm; 8 = 500 μ m.

MATERIAL: **Namibia:** Kunene River, 1 specimen, Stein Guard Post, riffle, 17°25'55"S, 13°59'05"E, 12.xi.1997, F.C. de Moor & S. Bethune (KUN16F); 7 specimens, same except: hand-collected off stones in slow current, 12.xi.1997, F.C. de Moor (KUN18F) (AMGS).

TAXONOMIC NOTES: Similar to *E. ferruginea*, but differing in the following respects: *E. ferruginea* has the valves relatively higher and shorter than in *E. parasitica*; *E. ferruginea* has 8–14 growth

Table 1. Occurrence of bivalve species in the seven major river and wetland systems of Botswana and Namibia.

Genus & species	Kunene River	Okavango River	Okavango Delta	Eastern Caprivi wetlands	Upper Zambezi River	Limpopo River	Gariep (Orange) River
<i>Aspatharia pfeifferiana</i>	+	+	+		+		
<i>Coelatura kunenensis</i>	+	+	+	+	+		
<i>C. mossambicensis</i>						+	
<i>Corbicula fluminalis</i>	+	+	+	+	+		+
<i>Etheria elliptica</i>	+						
<i>Eupera ferruginea</i>		+	+	+			
<i>E. parasitica</i>	+		+				
<i>Mutela zambesiensis</i>	+	+	+	+	+		
<i>Pisidium reticulatum</i>			+				
<i>P. viridarium</i>			+				
<i>Chambardia petersi</i>						+	
<i>C. wahlbergi</i>	+	+					
<i>Sphaerium capense</i>		+	+	+			
<i>S. incomitatum</i>		+	+	+			
<i>Unio caffer</i>							+
Total no. of species	7	8	10	6	4	2	2

lines per millimetre (measured in the middle of a valve), whereas *E. parasitica* has 14–16 (Appleton 2002). The KUN specimens (listed above) have 15–24 (*mean*=20) growth lines/mm and the largest specimen measures 4.1 x 3.0 x 1.9 mm. Only one of these Kunene shells has a pattern of radiating dark flecks, usually apparent in the genus in other river systems (e.g. the Okavango system); the remainder are all uniform cream/yellow. Although such uniform pale colouration has not (to our knowledge) been previously noted in southern Africa, Mandahl-Barth (1954), does note this character in both his generic and species descriptions. Mandahl-Barth (1988) later regarded *E. parasitica* to be a synonym of *E. ferruginea*. There is thus debate over the taxonomic position of this species which, if it is considered valid, is distributed over eastern and northern Africa. These are the first records from southern Africa. The name *parasitica* may relate to the way *Eupera* uses its byssus threads to attach to submerged surfaces such as vegetation (Appleton 1977), or cavities in *Etheria* valves (Pilsbry & Bequaert 1927).

DISCUSSION

A total of 18 species of freshwater bivalve has been reported from Botswana and Namibia. In most cases these are well-described, but some revision may be necessary in respect to the four species and/or genera: *Coelatura kunenensis*, *Eupera*, *Mutela zambesiensis* and *Pisidium*. Appleton's (1979) morphological comparison of *Coelatura* from the Kunene, upper Zambezi and Kafue Rivers, on the one hand, and the Okavango

system on the other, should be extended and pan-African reviews of *Eupera* and *Pisidium* are also desirable.

New morphometric data are presented for *Mutela zambesiensis* and *Spathopsis petersi*. The latter is uncommon and the published description of the former is brief; Mandahl-Barth (1988) noting that it requires better characterisation. The additions to the description of *M. zambesiensis* are based on the study of the morphometry of a West African iridinid, *Aspatharia sinuata*, by Blay (1989). Blay demonstrates a coefficient of variability of <10% in the mean length:height ratios of shells of both sexes and different sizes from five widely separated habitats in Nigeria, three lotic and two lentic. He interpreted this limited between-habitat variability in shell dimensions as indicating a relatively small environmental effect on an otherwise stable shell form for the species. Assuming this to apply to other Iridinidae, the H vs. L regression equations provided by Daget (1962, 1964), for West African species of *Aspatharia* and *Mutela* respectively, may be useful in separating several species of the two genera, and hence, in defining *M. zambesiensis*. This is somewhat at variance with the widely held view that habitat diversity and instability have, by promoting reproductive isolation, led to variation in shell form in freshwater molluscs at the subspecific or variety level, but are too short-term to have resulted in speciation. It could be argued, however, that such intra-specific variability is more likely to be a characteristic of pulmonate gastropods than of bivalves, as the former have colonised a greater range of habitat types over a wider geographical area and have much shorter generation times.

In terms of diversity, the bivalve fauna of the northern areas of Namibia and Botswana is a rich one. This is probably because, as noted earlier, the drainages involved extend into central Africa and abut the species-rich Zaïre system. Table 1 illustrates the

Table 2. Bivalve species reported from south-central Africa, arranged in three categories, based on known distribution patterns. These categories differ from those used for the gastropods of the Okavango system by Brown *et al.* (1992).

1. Species widely distributed in tropical/sub-tropical Africa (50%)	2. Species distributed in southern and south-eastern Africa (39%)	3. Species confined to south-central Africa (11%)
<i>Aspatharia pfeifferiana</i> <i>Corbicula fluminalis</i> <i>Etheria elliptica</i> <i>Eupera ferruginea</i> <i>E. parasitica</i> <i>Pisidium casertanum</i> <i>P. ovampicum</i> <i>Chambardia wahlbergi</i> <i>Sphaerium capense</i>	<i>Chambardia petersi</i> <i>Coelatura mossambicensis</i> <i>Pisidium langleyanum</i> <i>P. reticulatum</i> <i>P. viridarium</i> <i>Sphaerium incomitatum</i> <i>Unio caffer</i>	<i>Coelatura kunenensis</i> <i>Mutela zambesiensis</i>

occurrence of 15 species in the seven major river/wetland systems in Namibia and Botswana. The other three species, *Pisidium casertanum*, *P. langleyanum* and *P. ovampicum*, have only been sampled from isolated marshes and springs in the interior of Namibia.

The Okavango River and Delta support the greatest diversity, with eight and 10 species respectively, including three species of Sphaeriidae in the former and six in the latter. These tiny bivalves are best collected from sieved sediment samples, but as far as the writers are aware, this has only been undertaken in the Okavango Delta. Indeed, the finding of three sphaeriid species occurring sympatrically in the sediments at one station on a slowly-flowing channel in the Okavango Delta (Appleton *et al.* 2003), is evidence that they are more common in the area than previously thought. Neither *A. pfeifferiana* nor *C. wahlbergi* is widespread in the study area, but the absence of the latter from the Okavango Delta and upper Zambezi, and the former from the Eastern Caprivi wetlands, may simply reflect inadequate sampling in these systems. The presence of the river oyster *E. elliptica* only in the Kunene is, however, likely to be true, as the rapids and waterfalls that constitute its habitat are uncommon in the other rivers. With these points in mind, it is useful to note that Brown *et al.* (1992) reported five gastropod species as occurring in the Okavango River, but not in the Okavango Delta. That number has since declined to two with the finding of *Bulinus tropicus*, *Melanoides victoriae* and *Segmentorbis kanisaensis* in the Delta by Curtis (1997) and Appleton *et al.* (2003).

With the exception of *Pisidium casertanum*, *P. langleyanum*, *P. ovampicum* and *Unio caffer*, the species here constitute a largely tropical assemblage, concentrated in the rivers systems forming the northern borders of the two countries, viz. the Kunene, Okavango and Zambezi systems. One species, the river oyster, *Etheria elliptica*, reaches the most southerly limit of its range in the Kunene River on the Namibia/Angola border, while two others, *Aspatharia pfeifferiana* and *Coelatura kunenensis*, do so in the Okavango Delta in Botswana. Neither occurs in south-eastern Africa, although *A. pfeifferiana* was reported from Zimbabwe by Connolly (1939). *Mutela zambesiensis* occurs in all three large river systems in the study area, and small samples of *Mutela* collected by C.H.J. Schutte in the 1970s and the late A.C. Evans in 1988 in the *lowveld* of Mpumalanga Province, South Africa, suggest that it may be distributed more widely across the sub-continent. Until recently the only localities where *Pisidium* had been recorded were isolated springs in the Grootfontein District of Namibia, but the finding of two species in the Okavango Delta (Appleton *et al.* 2003), indicates that these small bivalves are more generally distributed and future collecting should target them. Kuiper (1965) described a new species of bivalve, *Micranodonta regii* (family not established), from the Waterberg area of north-eastern Namibia, but this was a misidentification. The shells illustrated are those of a conchostracan crustacean belonging to the family Cyzicidae, probably *Caenestheriella australis* (Lóven, 1847) (M.L. Hamer pers. comm. 1997).

The zoogeographical affinities of the freshwater bivalve fauna of Namibia and Botswana appear to reflect three components (Table 2). These being 1) a tropical/subtropical African component, including species distributed widely across tropical and sub-tropical Africa and occurring in the Zaïre River system immediately to the north of the study area; 2) a southern and south-eastern African component; and 3) a small regional 'south-central African' component.

Less than half (44%) of the species recorded from the study area also occur immediately to the north, in the Lake Bangweulu-Luapula River basin in northern Zambia (Mandahl-Barth 1968). This list includes only three of the eight unionoidan bivalves listed in Table 2, *A. pfeifferiana*, *C. wahlbergi* and *E. elliptica*, which for the two iridinids may reflect the dispersal of their host fish during their parasitic larval phase. It is not known whether *E. elliptica* has a parasitic larva. Furthermore, six of the species present in the Bangweulu-Luapula system are categorised as 'tropical/sub-tropical African species' in Table 2, three as 'southern African species', at the northern limit of their ranges, but none as south-central African endemics. The three species in category 1 not found in this adjoining system are all sphaeriids which are, as noted above, small and often missed.

Endemism among bivalves is low in the study area, i.e. only the two unionoidan species constituting category 3 above, especially when compared to the Zaïre River basin, in which Dudley (2001), estimated there are 14 endemic species. It may be no coincidence that these two are both in need of taxonomic revision, and that one, *M. zambesiensis*, may extend into eastern South Africa. It is tempting to attribute the restriction of *C. kunenensis* and *M. zambesiensis* in south-central Africa to fish host-specificity, resulting in fewer opportunities for dispersal. However evidence from a study of the reproductive biology of unionoidan bivalves from Lake Kariba (Kenmuir 1980a, 1980b, 1980c) suggests, both from experiments and field catches, that these bivalves may not be rigidly host-specific and may use a variety of fish species as hosts. Most of these belong to the family Cichlidae. *Mutela zambesiensis* also develops on a mormyrid. An exception may be *C. wahlbergi*, which failed to develop on several cichlid species or on *Barbus* sp. (Cyprinidae). This led Kenmuir (1980a) to suggest that *C. wahlbergi* may be more host-specific than other species. This may have implications for its dispersal and may explain its limited distribution in the study area (Table 1).

The fish fauna of the Okavango system is similar, in terms of species present, to those of the adjacent upper Zambezi and Kunene river systems, sharing 96% and 54% of species with these systems respectively (Skelton *et al.* 1985). In addition, all the species cited by Kenmuir (1980a) as hosts for larval *C. mossambicensis* and *M. zambesiensis* in Lake Kariba are also widespread in the Okavango. This similarity may be explained by links that either exist today, or have done in the past, between the Okavango and other river systems in the region. Very tenuous links exist across hundreds of kilometres of

currently dry terrain between the Okavango and the Kunene *via* the Cuvelai drainage and with the upper Zambezi *via* the Selinda Spillway and Eastern Caprivi wetlands (Skelton *et al.* 1985). More substantial links existed between these systems in the past and also between the Okavango and Limpopo and Gariep (Orange) rivers. A valuable discussion of the past links between the river systems in the study area was provided by Dudley (2001), and may be summarised by his concluding comment that ‘... *during the Pleistocene, extensive parts of the central African plateau were connected hydrologically and wetland organisms had an easy means of dispersal across them.*’

A zoogeographical map of Africa based on freshwater mollusc distribution (van Damme 1984), shows the study area occupying most of the western and central parts of the ‘Angola-Zambesian’ district of the ‘South African Province’, which in turn forms part of the ‘East & South African Subregion’. As with Dudley’s (2001) review, this draws attention to the fact that the Kunene-Okavango and Zambezi basins form a ‘cross-way’ of fresh waters running from west to east across the continent. This conduit provided access to the sub-tropical lowlands of south-eastern Africa and may account for the low endemism among bivalves in the study area.

Distribution patterns may change however. Curtis (1999) has provided important evidence that two species, *Corbicula fluminalis* and *Etheria elliptica*, have been introduced from the Kunene River into the Calueque-Olushandja canal in north-west Namibia, and *C. fluminalis* into the associated oshanas and the Cuvelai basin as well. *Coelatura kunenensis* also occurs in these oshanas. This is significant because it suggests that the predicted translocation of molluscs *via* the system of inter-catchment canals being built in northern Namibia from both the Kunene and Okavango rivers to dams in the country’s interior (Bethune 1985; Bethune & Chivell 1985) has become a reality.

Whether *C. kunenensis* occurs naturally in these oshanas is not clear, but van der Bank (1995) showed using enzyme electrophoresis that this species (from the Zambezi River above the Victoria Falls) had a heterozygosity value (H) of 7.5%; the first such measurement for any African bivalve species. The author noted that $H=7.5\%$ was relatively low compared with data from non-African freshwater bivalve populations and may be a consequence of the inherent instability of African riverine habitats and those associated with rivers, e.g. the oshanas where Curtis (1999) collected *C. kunenensis*. The restoration of populations after periods of drought or flood will rely on immigration from refugia within the system, or reproduction by residual founder populations, and this could create recurrent genetic bottlenecks that would be compatible with this finding.

Little is known of the biology or ecology of freshwater bivalves in southern Africa. Kenmuir (1980a, 1980b, 1980c) provided unique data on the standing stocks and reproductive biology of three unionacean species (*Chambardia wahlbergi*, *Coelatura mossambicensis* and *Mutela zambesiensis*) in Lake Kariba, Zimbabwe. Although bivalves can become the dominant members of the benthos of freshwater habitats, they are

sedentary animals and are thus severely affected by droughts when water levels drop. Some, such as *C. wahlbergi*, are able to survive periods of desiccation of up to 2½ years (Cockson 1971), but many die during droughts. Such large-scale drought-related mortalities allowed Marshall (1975) and Appleton & la Hausse de Lalouviere (1987) to measure the population densities of *Coelatura framesi*, *C. mossambicensis*, *C. wahlbergi*, *Corbicula fluminalis* and *M. zambesiensis* in the exposed sediments of Lake Chivero (formerly Lake McIlwaine) in Zimbabwe and the Pongolo River floodplain in South Africa. Appleton *et al.* (2003) presented data on the population densities of *C. kunenensis*, *M. zambesiensis* and *C. fluminalis* in the Okavango Delta, relative to the grain size composition of the sediments in which they were living.

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ERRATUM

In the paper ‘Chironomidae (Diptera) in the Albany Museum’ by A.D. Harrison in the *Annals of the Eastern Cape Museums* Volume 2: 2001 [2002] pg. 12 first column under ‘SPECIMENS EXAMINED’ lines 5 and 6 should read “... 3 ♀ Klein Mooi River, below Mooi River Falls, 29.06S 30.30E, 4 iv 1995 (cat. MOI 37AF v, vi, vii), 1 ♂ Mooi River, on Dalcrue Farm, 29.36S, 29.89E, KwaZulu-Natal 4 i 1996 (cat MOI 65CA), collectors F.C. de Moor and team.”

Annals of the Eastern Cape Museums

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The editors of the *Annals of the Eastern Cape Museums* invite papers and short articles in the fields of the natural and human sciences. The primary objective is to publish the results of research undertaken by staff of Eastern Cape museums, and by researchers whose results are wholly or partly based on material housed in these museums. Other papers of broader interest in the Afrotropical Region shall also be considered at the discretion of the editors. English language manuscripts are preferred, although contributions in other languages may be accepted at the discretion of the editors. All submitted manuscripts are reviewed by at least two external referees. There are no page fees or limitations on length, but authors able to provide complete funding for publication can be guaranteed publication of accepted manuscripts in the first following issue.

Submissions: Only electronic submissions are acceptable. Submit manuscripts as Word documents or in Rich Text Format (rtf), either as e-mail attachments, or burnt onto a CD Rom. Figures should initially be sent as low resolution jpeg files for the refereeing process. Authors should liaise with the editors as to system compatibility for final submission of illustration files. Text formatting should follow these instructions, with document formatting kept simple without imbedded internal style or other documented formatting, complex tab stops, etc. For example, end notes and acknowledgements should be typed on the appropriate pages and not included as internal text and a single text style should be applied throughout, without 'headings' formats, etc.. Submitted manuscripts which do not conform to the Instructions for Authors or which require extensive English language editing shall be returned. The first author is responsible to ensure that the final content of manuscripts is agreed upon by all co-authors.

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